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STUDIES ON ENCHYTRAEIDAE

2. Field Studies

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This second paper of a series dealing with the ecology of Enchytraeidae presents the results of a one-year census in some fifty stations covering a wide variety of Danish habitats. The chief purpose of the investigation was to obtain a general idea of the numbers of Enchytraeids encountered in various habitats, their biomass and seasonal fluctuations, and to single out at least some of the factors responsible for the density variations in time and space. In future papers these factors will be dealt with in greater detail.

In order to facilitate comparison, the results of the present investigation are presented in a way similar to that employed in the author's paper on free-living nematodes (1949).

1. MATERIAL AND METHODS

The census work was carried out during the period from Oct. 1953 to Nov. 1954. Throughout this year approximately fortnightly sampling took place in 4 stations, each comprising c. 100 sq.m of apparently homogeneous ground selected so as to be typical of the appropriate habitats. In two additional stations regular sampling took place from the summer of 1954 onwards. The habitats in their turn were defined on the basis of their vegetation and certain edaphic factors which seemed to be important. The set of data obtained in this way supplied the chief information on the seasonal variation in numbers and on certain other problems. The six stations in question are all in an area of identical geological origin while each of them show different pedological, microtopographical, and botanical features which will be outlined below.

In addition to this detailed census-taking further sampling took place in 42 stations which were visited less regularly, some even once only. This collection of data provided the chief information on the differences in population density in a large number of habitats at periods scattered throughout the year.

On each visit to a station one sample was taken (in a few cases more than one) consisting of 15 sample units each of 41 sq.cm area. The calculation of the population density of the entire profile was carried out directly on this basis and on supplementary information on the type of vertical distribution of

Enchytraeids in the various stations and at various times of the year derived from special sampling. The height of the soil cores was five cm, and all sampling was carried to such a depth that appr. 75 % of the total population would fall within the sampling depth. In most cases one slice of 5 cm would suffice to attain this standard but in some stations the type of vertical distribution necessitated an extension of the sampling to greater depth by removing further slices of 5 cm each.

The lots of 15 sample units were taken to the laboratory and extracted without delay according to the technique already described (Nielsen, 1952-53). In case the ground was frozen the sample was left in the laboratory for 24 hours prior to extraction.

The material on which the investigation is based amounts to 3375 sample units with a total of 424119 Enchytraeids.

The live weights quoted refer to the mean live weight of Enchytraeids without gut contents, and they were arrived at as follows: The Enchytraeids extracted from the cores were transferred individually by pipette to Petri dishes where they remained for two days at appr. 15° C. By then they had emptied themselves of gut contents and were again transferred individually by pipette to a watch glass removing, through repeated transfers and washings, all traces of soil particles and other contaminants. The greater part of the water was pipetted off and the remainder sucked off with filter paper. When only a thin film of water remained the worms were arranged in a small heap by means of needles and afterwards pressed lightly by strips of filter paper until no more water could be extracted from them. In this condition the batch of worms could be handled in toto as a ball, and with a needle it was transferred to the pan of the balance and weighed to the nearest 0.1 mg. From each sample so many units were used for the weighing that the total of worms would amount to appr. 1000 individuals. They were weighed as five lots each of them comprising the worms from one or more sample units. All worms from one unit were always weighed together, such that no errors due to selection would creep into the material. Samples containing less than 1000 worms were weighed in five lots comprising three units each and matched so as to be of nearly the same size. Of course, it was possible to weigh only a small proportion of the material because the process is very time-consuming. However, a fair selection has been made so as to cover a good many stations at three different periods of the year. Because of accidental circumstances it was necessary to interrupt the weighing during part of the summer of 1954.

The technique does not claim any high degree of accuracy, however, it is believed to be sufficiently accurate for the purpose. Possibly an insignificant amount of water may still be present in the capillary interstices between the worms, but on the other hand it is also possible that small amounts of mucus adhering to the epithelium of the worms have been removed by the filter paper; also the fact that the worms were stored in tap-water should not be overlooked as a source of error. In spite of these possible inaccuracies the method was adopted as the only practicable one, and in all cases the worms were treated in exactly the same way, such that the relative weights can be considered reliable even if the absolute weights may deviate slightly from the true weights. One batch of worms carried through the entire process from storage in water to the actual weighing six times showed weights reproducible within 2.6 mg (37.9; 37.1; 35.3; 36.4; 36.0; and 36.8 mg respectively).

The taxonomy used in this paper is based on Ude (1929). In a few cases the species as conceived by me show minor deviations from the characters mentioned by Ude (l. c.). In such cases reference is made to Christensen and Nielsen (1955) where a preliminary discussion of some taxonomical problems is given using the same species concept as here and supplemented by chromosome data. In later papers the taxonomical problems will be dealt with at greater length.

2. SEASONAL VARIATION

1. Description of stations 1-6

The population density of Enchytraeids proved to undergo drastic seasonal fluctuations, a fact to be kept in mind when comparison is made between populations of different habitats.

As mentioned already the seasonal variation was studied in detail in six stations. However, before giving an account of the findings, the area in which these station were located is described in some detail.

The area belongs to the Mols Laboratory and borders on Ebeltoft Vig. It consists of a low lying stretch of land which was raised above sea level during the general upheaval of northern Denmark commencing during the Stone Age. Since then the upheaval has been succeeded by a general accretion of land caused by current and wave action in Ebeltoft Vig. It is not possible to make any sharp distinction between the two processes. The land in question is between the present day and the ancient (Stone Age) coast line which latter is marked by the steep slopes forming the eastern boundary of the sandy and gravelly (in some places clayey) Ice Age moraines. The total width of this raised Littorina sea bed amounts to 300-700 m as far as the grounds of the Laboratory are concerned (in other parts of the Mols peninsula the width varies between 0 and 900 m). Brief descriptions of the area, partly with photos, are given by Thamdrup (1947-48).

Weis-Fogh (1947-48) and Nielsen (1949). In the present connection chief interest is attached to the inner part of the area, i. e. the part along the foot of the ancient coast line, locally known as Sletten (The Plain), and some of the copses farther toward Ebeltoft Vig.

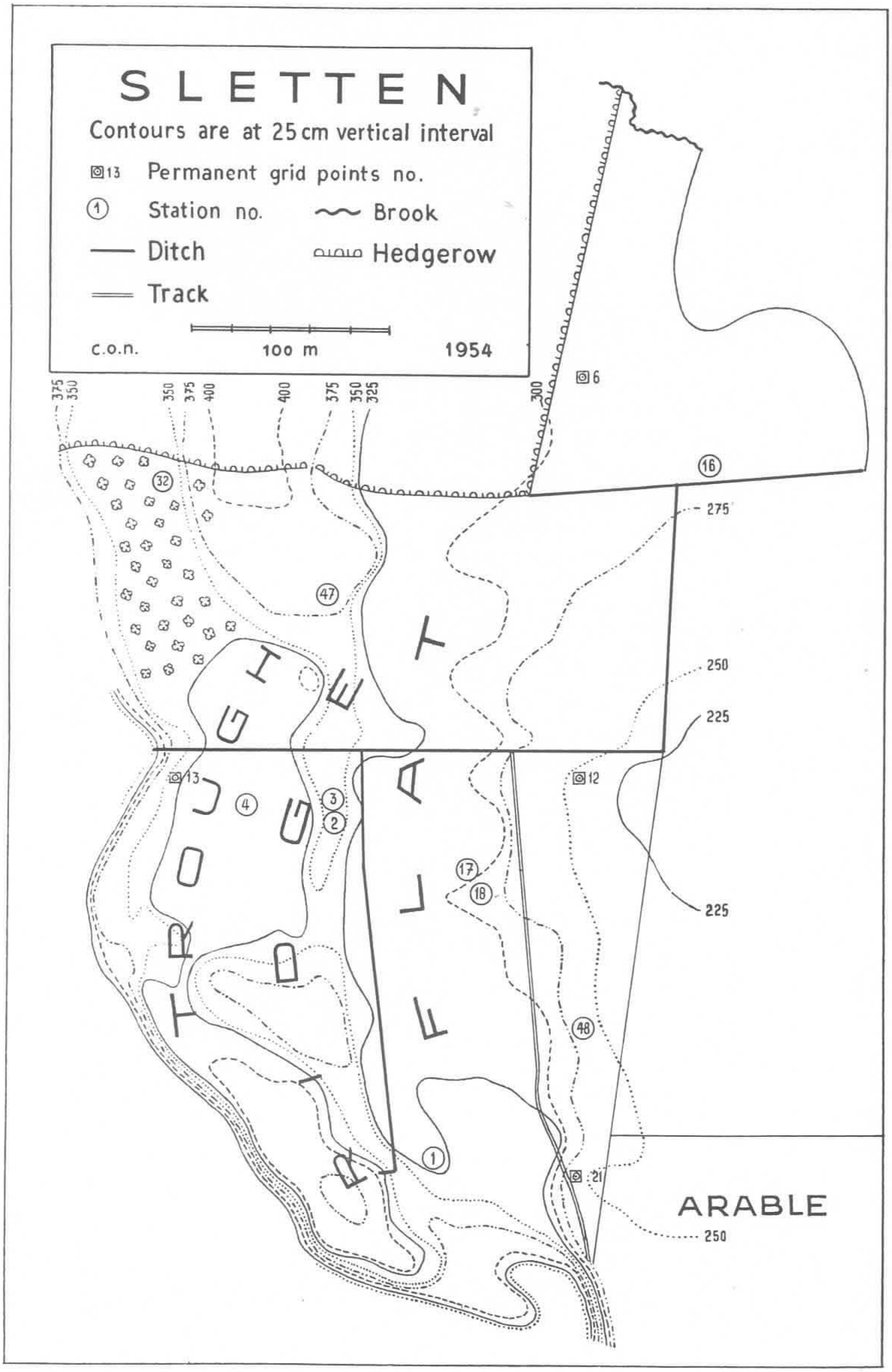
The general location of the area appears from the map given by Thamdrup (1. c.) where the broken line through column E of the grid system indicates the ancient coast line. Sletten comprises the greater part of the quadrats D 3 and 4, while the copses cover the greater part of the quadrats C 3 and 4.

In Fig. 1 is presented a detailed map of Sletten proper made for this particular investigation. The contours, some landmarks and the location of the stations are shown together with the permanent grid system.

The contours were traced using a 10×20 m grid for the surveying. Their general course is seen to be longitudinal from S towards N, i. e. parallel to the ancient coast line. Schematically the area consists of a ridge above the 325 cm contour rising up to 400 cm in the broader northern and southern parts while the elevation reaches a maximum of c. 340 cm in the narrow middle part. This high ground will be called the Ridge in this paper. West of the Ridge, separating it from the ancient coast line, is a depression (elevation less than 350 cm, the minimum being c. 270 cm), this area will be called the Trough in what follows, and it is immediately at the foot of the ancient coast line from which slopes rise steeply up to 20-35 m above sea level. East of the Ridge the ground falls off gently until the copse is reached at the 225 cm contour. The stretch E of the Ridge will be called the Flat. It continues eastwards to the present day coastline. Superimposed upon the general falling off are two or three minor ridges separated by depressions. The most easterly depression is occupied by a bog, Ålen, where sampling has also taken place (stations 5, 33). In the copse, Åbuskene, NE of the Plain is situated st. 6.

Physically the soil of the entire raised Littorina floor is sandy. The matrix of the soil may well be drift sand as far as the mechanical composition is concerned. In many places c. 90 % of the particles fall within the size range 0.2-0.6 mm with only c. 1 % of particles less than 0.002 mm. In other stations (st. 1) particles > 0.6 mm contribute c. 46 % and the 0.1-0.6 mm group c. 40 % (according to analyses by dr. Køie, quoted from Weis-Fogh (1. c.)). In general the sand is coarser on the Ridge than in the depressions. Morphologically the dominant category is rounded quartz grains.

Into this matrix is woven a variable amount of *organic matter* more so in the depressions than on the ridges. The cause for this is obviously the improved water supply in the depressions which has made possible a more luxuriant vegetation and a quicker rate of accumulation of organic matter and correspondingly higher root content.


SLETTEN
Contours are at 25 cm vertical interval
◎13 Permanent grid points no.
① Station no.
Brook
Ditch
Hedgerow
Track
c.o.n.
100 m
1954
375
350
350
375
400
400
375
350
325
300
275
250
225
225
250
TROUGH
RIDGE
FLAT
ARABLE
32
47
16
4
3
2
17
18
48
1
6
13
12
21

The organic matter content is c. 2-4 % of the mineral weight on the Ridge, c. 20-25 % in the Trough and on the eastern part of the Flat while on the western part of the Flat it is 10-15 %, all percentages referring to the upper 5 cm of the profile.

The *water content* is difficult to circumscribe because of the wide fluctuation during the year. However, in the Trough and at the eastern border of the Flat the ground water level is so high that even during prolonged dry spells water will be available in the upper layers due to capillary rise from the ground water. On the Ridge the ground water level sinks during the summer and is often below one meter depth, i. e. capillary action cannot supplement the water content of the upper layers should precipitation be too low. Because of the wide fluctuations in ground water level during the year it is correcter to consider the Ridge an area regularly exposed to drought conditions and the Trough and eastern part of the Flat areas rarely exposed to drought. During the period late autumn-early spring the southern part of the Trough is always flooded, the northern end of the Trough and the eastern border of the Flat normally so. Farther east the bog holds water during the greater part of the year, the water only sinking during midsummer in most years and so exposing the dried-up mud flats. As an example of the fluctuation in water content during the year the following data illustrate the water percentage (% of dry weight) on the Ridge on two different dates, one in the autumn of 1953 and one in the drought period of the summer 1954. They do not tell much about the availability of water but give some idea of the seriousness of the fluctuations.

TABLE 1

Depth	**% water**	
cm	29. X. 53	2. V. 54
0—5	17.0	1.9
5—10	9.4	1.8
10—15	11.3	1.3
15—20	13.6	0.8
20—25	16.4	1.1
25—30	21.3	1.6
30—35	22.0	2.9
35—40	22.6	3.0
40—45	23.2	3.7
45—50	23.7	4.8
50—55	23.8	6.0

The *pH* varies from c. 4.0 to 5.8, however, the detailed distribution of pH values was not studied, only it is mentioned that values round 4.0 seem to predominate in the *Calluna* vegetation.

Recent history. Up to about 1875 the entire Littorina area was used for agricultural purposes. The Trough was artificially drained into the bog, Ålen, by means of a transverse ditch still existing but not conducting any water, and from the bog a drainage ditch led into the brook farther North. By then the area comprising the copses and right down to the present coast line was used for grazing while Sletten proper was arable land much like the area S of the copse. The copse Åbuskene was woodland already then. A little later the pasture was abandoned and the copse has come up during the 75 years since then. For some years still Sletten was cultivated gradually larger areas being employed for grazing until about 35 years ago the last part was abandoned as arable land (the part of the Trough just S of grid point 13, however, carrying rye in 1937 and 1938). Since then Sletten has been a permanent pasture used for grazing heifers and it has never been fertilized nor limed. During the last ten years the stock grazed during the summer amounts to 6-10 head but earlier the stock was larger. Following the decreasing grazing pressure certain changes in the vegetation have taken place, the most conspicuous feature being the invasion of scattered junipers on the high and medium high ground. Recently the spread of *Calluna* has followed, especially in the areas already occupied by juniper, i. e. a longitudinal stretch from the copse westwards to beyond the N-S track and with a branch from the SE corner along the Ridge. Between the two branches scattered *Calluna* occurs in many places and, were nothing done to prevent it happening, the entire area except perhaps the Trough would be covered by *Calluna* in a few years. Along the W margin of the copse a self-sown birch-willow-bramble scrub is spreading rapidly, now roughly following the 250 cm contour.

The *vegetation* reflects fairly well the microtopography of the area. The upper part of the Ridge is dominated by *Agrostis canina, Jasione montana, Hieracium pilosella, Helichrysum arenarium, Polytrichum piliferum, Cladonia* spp. and *Peltigera* spp., all of them being drought resistant. On the southern part of the Ridge *Calluna* is the sole dominant while on the middle and northern part it occurs as clumps scattered between the vegetation just mentioned.

On the lower part of the Ridge and the upper part of the Flat the species mentioned become less abundant and are gradually supplanted by *Sieglingia decumbens, Agrostis tenuis, Luzula campestris, Euphrasia* sp. *Stereodon cupressiforme, Dicranum scoparium* and *Hylocomium squarrosum.* Also here *Calluna* dominates in some places forming larger or smaller patches. In the Trough and towards the eastern part of the Flat another set of plants takes over dominance while the species dominating on the Ridge entirely disappear and the dominants from the intermediary areas become less abundant. Here the dominants are *Carex demissa*, *Brunella vulgaris*, *Pedicularis palustris*, *Bellis perennis*, *Hieracium auricula*, and *Acrocladium cuspidatum*.

In addition to the species mentioned a large number of other plants occur which may be quite conspicuous, however, for purposes of characterizing the areas they are not important as their density is low.

In Åbuskene oak, hazel and alder dominate with *Anemone nemorosa* in the field layer.

The bog, Ålen, is dominated by *Myrica*, *Carex* spp., *Erica Tetralix* and surrounded by birches with *Calluna* in the glades.

The northern part of the Trough is occupied by a small ash-hazel-willow woodland with *Anemone nemorosa* and *Adoxa moschatellina* as important members of the field layer.

As a supplement to what has been said here reference is made to Weis-Fogh (l. c.). Much of what he says about his station Pl. I will also apply to the Ridge, and the upper part of the Flat (where his station is located). Pl. VII would in many respects correspond to the Trough and the lower part of the Flat. The intermediary levels would with some approximation correspond to his stations Pl. IV-VI. In Thamdrup (l. c.) Fig. 18 is a view across the middle part of Sletten just South of the transverse ditch. The view is from the ancient coastal slope towards the present-day coast. St. 4 is just in front of the three resting heifers in the left middleground. Weis-Fogh's stations are behind the same three heifers half way between the longitudinal ditch and the copse. Immediately in front of the copse a row of low bushes can be distinguished, they have by now developed into the fairly solid birch-willow-bramble scrub mentioned above. A photo of Ålen is given in Fig. 17 of the same paper. The southern part of the Trough (flooded) and the Ridge (left) is shown in Fig. 25 of Weis-Fogh's paper. St. 1 is behind and a little to the left of the cow.

The position and characteristic features of stations 1-6 are as follows (see Fig. 1, where the numbers indicate the position of the stations).

St. 1. Upper part of Flat, c. 320 cm elevation. Dominant vegetation:*Sieglingia decumbens*, *Agrostis tenuis*, *Hieracium pilosella*, and *Hylocomium squarrosum*. The vegetation is low but with a high degree of cover. During the summer of 1954 the drought had a striking effect on the plants.

St. 2. On the Ridge, c. 365 cm elevation. Soil consists of sand with c. 2 % organic matter. The samples were taken in very dense *Calluna* tufts of 50-100 cm diameter. No other vegetation.

St. 3. Same location as st. 2 but in the vegetation surrounding the *Calluna* tufts: *Agrostis canina*, *Hieracium pilosella*, *Polytrichum piliferum*, and *Cladonia* spp. dominating. Cover very scanty. In spite of the very hardy plants the effect of the drought was still more conspicuous than in st. 1.

St. 4. In the Trough, c. 310 cm elevation. Soil rich in organic matter. Dominant plants: *Craex demissa, Bellis perennis* and *Acrocladium cuspidatum.* During the drought period the soil was distinctly drier but no effect on the vegetation was noticeable.

St. 5. Beside the bog, Ålen, in *Calluna* clump of 8 m diameter in a glade between birches. Elevation c. 125 cm. Soil rich in organic matter. Sole dominant: *Calluna.* No drought effect during the summer.

St. 6. Åbusken. Elevation c. 160 cm. Among oak-hazel litter. No vegetation except *Anemone nemorosa* in the vernal aspect. Soil rich in organic matter. No drought effect during the summer.

2. *Results*

In each of the six stations described sampling took place at short intervals in order to follow the seasonal variation in places with very different environmental factors.

The mean number of Enchytraeids per sample unit in the layer 0-5 cm depth is presented for each sampling in Table 4 (p. 28) and in Fig. 2. Additional information on the seasonal variation is afforded by the data from certain other stations, however, because of the less frequent sampling there the discussion of the extent of seasonal variation will be based on the results from the six stations exclusively. It must be mentioned that during the dry spell some downward migration may have taken place (cf. p. 17) but as this was on a very small scale and occurring at a time when the density was at its minimum, the minimum figures quoted here may be slight underestimates of the population, however, only to an extent that does not affect the order of magnitude.

By inspection of Fig. 2 (and Table 4) it is obvious that the numbers of Enchytraeids fluctuate violently during the year. Because of the random errors inherent in a material collected in the way adopted here it is not possible to discuss in detail the significance of the numerous smaller deviations from the general course of the graphs. In many cases the values obtained at time t were statistically significant from those found at time (t-1) but on the other hand the scatter of values within a single sample and between more samples taken simultaneously was too large to justify the assumption that statistically significant differences between successive samplings can be taken to mean that genuine changes in the population density had taken place during the interval between successive samplings. A more probable hypothesis is that even in such small stations

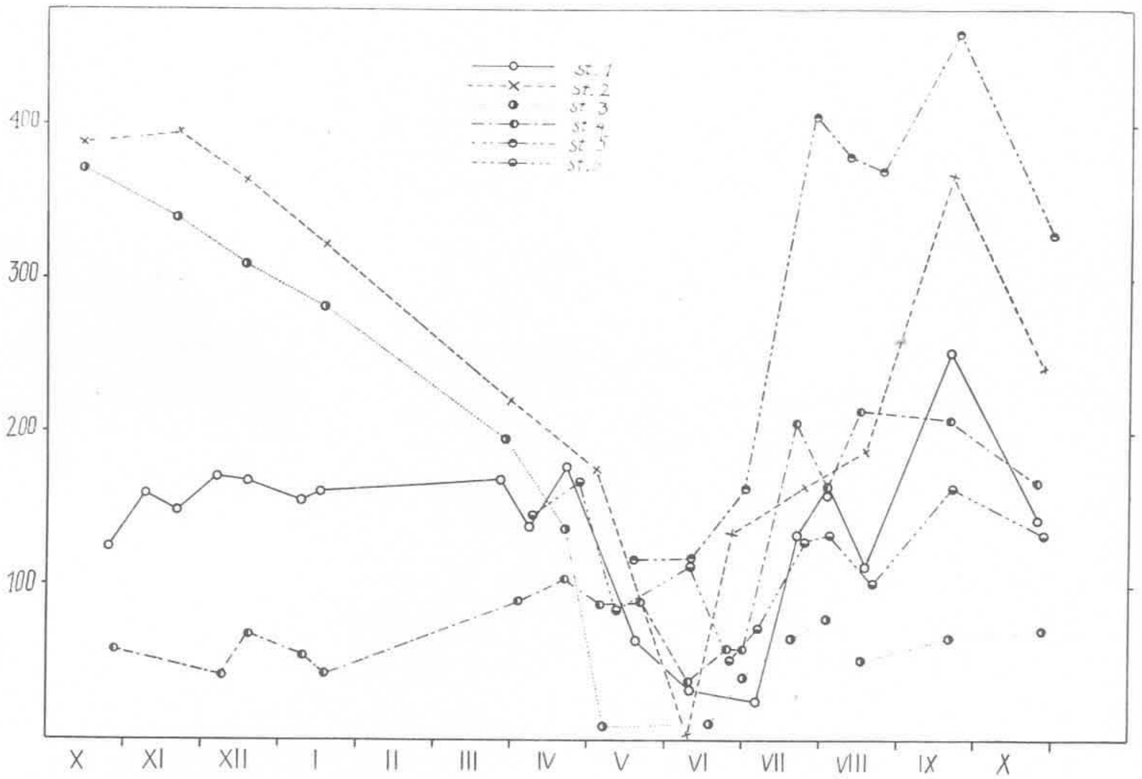


Fig. 2. Seasonal variation in density of Enchytraeidae in 6 stations, expressed in mean numbers per sample unit (cf. Table 4).

as employed here we are not dealing with simply one homogeneous population which can be characterized by a single mean density and standard deviation but with a multitude of populations with their individual parameters. Possibly they show density gradients originating in some primary center of multiplication but this is often obscured by alle degrees of overlapping and intergradation (see Nielsen, 1954). Because of complications of this nature the minor deviations from af smoothed curve will not be discussed here as it would require supplementary information not available.

Neglecting such unexplainable deviations one arrives at the following picture: All minimum values from stations 1-6 occur within the months May, June, and July. An inspection of Table 4 confirms this picture, as very few exceptions are found among the fairly large collection of data. It can, therefore, be concluded that the population density of Enchytraeids is at a minimum during the summer. For reasons mentioned on p. 20 greater precision is avoided until further evidence is available. Peak values are more difficult to define because of the smaller body of data available from autumn and winter. Hovewer, in the six stations where such values are at hand the position of peak values show a remarkable degree of similarity. In st. 1-3 and 5-6 the maximum density occurred during Sept. 1954 and in st. 4 in Oct. (1953).

The remaining stations (Table 4) display trends that do not militate against the findings from st. 1-6 as the highest values occur during the period early autumn-early spring but the sampling frequency was too low to define the exact position of the maximum. The conclusion is reached that maximum density of Enchytraeids occurs during early autumn (September-October).

As a consequence of the position of maximum and minimum values it follows that the curve depicting the seasonal trend becomes assymmetrical showing a slow decrease during late winter and spring and a rapid increase to maximum density. The period of decrease has a duration of appr. eight months (1 Oct.-1 July) and the period of increase only three months (1 July-1 Oct.). This fact was not apparent until a complete cycle had been followed and it could therefore not be studied specially. Hovewer, during the investigation certain data were collected which may contribute towards an explanation of the underlying mechanism. The problem is being studied in greater detail but until then the following hypothesis is offered as an explanation.

The chief reproductive season seems to cover the late summer and early autumn. This impression was based on the proportion of mature individuals present through the year. From late autumn throughout the winter until late spring it is often difficult to find mature individuals at all and, therefore, it is natural to assume that reproduction almost ceases during this period. The probability of this assumption is also supported by the low temperatures prevailing at this time. On the other hand a certain mortality must be operating, although it seems to be fairly moderate. Towards the summer reproduction commences to make itself felt but at the same time mortality reaches a maximum thus reducing the population to a small fraction of what it was a few months (or even weeks) previously. In spite of the very small population size with an exceedingly small percentage of mature individuals a rapid increase of population density takes place. The increase occurs so suddenly that the only probable explanation is afforded by mass hatching from cocoons already present in the soil. Some of these cocoons may have been deposited during the late spring (perhaps even during the late autumn) while others may be younger. Incidentally this would presuppose that the cocoons are better adapted to survive summer conditions than are the individuals already hatched. To what extent this holds true is under study. The mass hatching takes place immediately after the improvement of the soil water status. The mean weights during the year quoted on p. 45 prove that the outburst is really caused by the sudden appearance of newly hatched individuals, simultaneously with the population increase the mean weight drops to about one tenth of its size immediately before the minimum density is reached.

Another piece of evidence favouring the explanation just given is afforded by the speed with which the population increases. In two stations on the Ridge the following numbers were found per sample unit during the crucial period (15 sample units on each sampling date).

June				July		
2	14	21	30	8	19	26
7*)	68	117	177	244	329	
4	40	107	117			164

*) mean of 30 units

This hypothesis, if it is confirmed, would indicate that the crash during the summer results in an almost complete replacement of the population. One population consisting of a not very large proportion of mature individuals plus a preponderance of individuals of intermediary age is replaced by another one consisting of a very large number of newly hatched individuals plus an exceedingly small number of adults and upwards of one year old individuals. So far all pieces of evidence confirm the hypothesis. In st. 2 and 3 the virtually complete replacement is evident as respectively 1 and 3 % only of those present at the previous peak are still surviving when the minimum is attained. In other stations the reduction may be less drastic, however, this will be touched upon on p. 17. In any case there is no doubt that in all stations the tendency is the same although minor deviations may occur. The variation in mean size of the individuals throughout the year confirms the interpretation although this criterium suffers from the drawback that only the *size*, not the *age*, of the worms is considered, however, the assumption is probably sound that up to maturity the size is approximately proportional to the age.

The longevity of Enchytraeids under optimum conditions is not yet known (but it is being studied in cultures). However, there is every reason to believe that the maximum age is hardly ever reached in such places as st. 2 and 3. If the picture obtained through this one-year census is typical of the situation the probability for Enchytraeids to become more than one year old would seem to be very small, and as a matter of fact by far the greater proportion dies before reaching maturity.

This most extraordinary situation calls for an inquiry into the agents causing this colossal mortality. The author thinks that part of the explanation is immediately at hand. Table 4 shows that in all stations located in permanently moist areas the summer values of population density far exceed those in drier places. Admittedly the peak values are also often higher but the percentage mortality from peak to minimum seems to be directly related to the humidity status of the station. It is 99 per cent in st. 2, 97 in the supposedly more protected st. 3; in st. 1 is was 70 %, in st. 4 30 % and in st. 5 the minimum density as referred to the following peak suggests a mortality of appr. 60 %, all percentages being approximate only. It is not possible to express the moisture status of the stations in comparable units until tensiometer readings are available, therefore the only basis for comparison is afforded by the state of the plants during the drought period. In st. 3 the vegetation is fairly drought resistant (see p. 12) but in spite of this the above ground parts of the plants died off to a large extent while the soil was dusty dry. In st. 2 the heather seemed to survive but there was no flowering during the summer and many branches had no leaves. Because of the dense plant cover the assumption is made that the evaporation from under the heather was smaller than that from the almost bare ground between the open vegetation of st. 3. In st. 1 the drought was able to produce signs of desiccation of the plants, the rosettes of *Hieracium pilosella* were mostly curled up. In st. 4 and 5 the hygrophilic vegetation showed no signs of desiccation although, of course, the water content of the soil would have been reduced during the drought period. For en example of the degree of desiccation during the early summer reference is made to the determinations of water content of the soil near st. 3 presented in Table 1. It is immediately apparent that the amounts of water which have disappeared from the soil are very large indeed.

The author is convinced that the Enchytraeids were actually killed by desiccation, although of course it was not possible to demonstrate this directly. At any rate experiments have confirmed that Enchytraeids cannot survive even a few minutes stay in soil from st. 3 containing 2 % of water. Their cuticle is freely permeable to water and during the course of about half an hour would loose fatal amounts of water and could be recovered from the soil dead and dried up with a coating of sand grains cemented together by water and mucus extracted from their bodies.

Thus it seems to be a fact that in places where desiccation occurs at some time of the year the Enchytraeids will be killed off to an extent determined by the reduction of the free water content of the soil, and when a certain critical value is reached there is no possibility of surviving in loco. Theoretically they might escape death by migrating away from such threatened places. This might reduce the loss to some extent but no signs of actual horizontal migration have been noticed. Vertical migrations might produce the same effect, and actually they do occur but apparently on a small scale only. Statistically significant vertical migrations could be demonstrated during the beginning of the drought period but only from the horizon 0-5 cm into the next following 5-10 cm horizon. Further down the migration could not be traced, and if the worms only penetrate to about 10 cm depth they would gain little because the desiccation is at least as pronounced in this root zone. However, they may migrate farther down and die there, the method employed does not allow one to decide exactly *where* they died. In theory they might survive in the ground water zone, however, none are found living there either because they never reached this horizon or because they have reached it and afterwards died because of other reasons than desiccation (e. g. food shortage).

There are still some obscure points concerning the reactions of Enchytraeids to desiccation, however, the fact remains that in st. 2 and 3 the drought period was particularly severe, and as a matter of fact 97-99 % of the population died within a fortnight of the beginning of the drought period. They seemed to react by moving farther down to escape the unfavourable conditions. They were traced to 10 cm depth and may have reached deeper layers without finding possibilities for continuing existence. In other stations the degree of desiccation was smaller and the percentage mortality decreased accordingly. In stations not exposed to desiccation conditions would seem to favour higher population densities because of the reduced mortality during the summer. There are several indications that this holds true (Table 4), and from Fig. 2 it appears that the 1954 peak density seems to be about double the size of the 1953 peak corresponding to a reduced loss during the summer of 1954. As a contrast it is seen that the 1953 peak density in st. 3 was of the order of 400 per sample unit. The summer conditions caused a 99 % loss and the population did only succeed in building up a 1954 peak density of appr. 75 per unit. Of course, these facts may reflect random variations or some other explanation may be found, however, it is tempting to associate summer mortality and peak density as highly interacting phenomena. The population values will be followed in future and nothing definitely can be said about the question until more evidence is available.

It is not intended to postulate desiccation to be the sole cause of mortality, there may be several others. Thus in st. 1 there is a fairly dense populations of *Schendyla nemorensis* which, from observations and experiments, is known to feed a. o. on Enchytraeids, thus this predator will cause some loss. On the other hand desiccation must be a very important cause of mortality, in the author's opinion the most important one so far known in stations 1-3.

It is seen that in stations where the lack of available water cannot possibly be a mortality factor the population density also exhibits a summer minimum, although a few exceptions have been found. Therefore, some other factor must be operating. The best confirmation of this is afforded by Reynoldson's studies (1947, 48) of the Enchytraeid worm population of sewage bacteria beds. In this habitat a summer desiccation is out of question but in spite of this the two species *Enchytraeus albidus* Henle and *Lumbricillus (Pachydrilus) lineatus* Müll. showed pronounced seasonal fluctuations. Peak density (attributable to its habit of breeding most actively during the winter months coupled with smaller losses from washing out) occurred during the period Nov.-April. The peak was succeeded by low summer densities (indirectly caused by the destruction of its main food, the fungus *Oospora* sp. by larvae of *Psychoda alternata* Say). Reynoldson bases his conclusion on the numbers of Enchytraeids taken in food bags containing a bait consisting of 20 g of *Phormidium*, therefore absolute counts of worms per unit area (or volume) are not given, however, his curves and those given here (Fig. 2) are very similar. The minor discrepancies cannot be discussed because of the entirely different environments, e. g. it appears that the temperature in the sewage bacteria beds fluctuates within very narrow limits (c. 10° C during the winter — c. 20° C during the summer) which means that reproduction can (and actually does) take place throughout the winter. Winter reproduction is (in normal years) not possible in the habitats studied by me.

Because of Reynoldson's results and the author's findings in permanently humid habitats it seems likely that, although the proximate cause of mortality in stations 1-3 was certainly desiccation, a similar shape of the curve would result even if desiccation was excluded. However, the causative agents are unknown so far.

Before leaving the problem of seasonal fluctuations it may be important to stress the fact that the year beginning Oct. 1953 was very abnormal from a meteorological point of view. Until the end of March 1954 the water status of the soils was fairly normal with a high water content. On 3 Apr. 8 mm of rain put an end to what might be called the normal situation. From this day until 7 June when 7.5 mm rain fell, the total precipitation amounted to 6 mm (19 May) as compared with a normal rainfall during this period of c. 125 mm, thus the rainfall was about 10 per cent of the normal. On the other hand the last half of June, July and August had a rainfall by far exceeding the normal. The lack of rain during the period April to mid-June was accompanied by clear sky and consequent high temperatures which further accentuated the drought. Also the winter 1953-54 was exceptional in that very mild weather prevailed until the end of January. After this mild spell followed a period of frost (÷ 10-15° C) without interruption lasting for 28 days (28 Jan.-25 Feb.). Considering the long spell of frost (with negligible snow cover) it is worth to notice that no sudden decrease in Enchytraeid numbers occurred immediately after the frost receded which probably can be considered an indication that normal Danish winter conditions do not represent a critical period for Enchytraeids. They are able to survive without appreciable losses.

The summer conditions deviated from those of normal summers by the position of the dry spell and the sudden onset of rainy weather. In the areas of the Mols Laboratory summer droughts are of frequent occurrence but they normally occur later in the summer (July-Aug.) (see Weis-Fogh. 1947-48). Thus, while the occurrence of drought is fairly normal the general shape of the curves in Fig. 2 may be rather abnormal in that the period of decline is suspected to be of longer duration under normal circumstances. The sudden outburst of rain during late June and July would not normally occur until Sept.-Oct., therefore the position of the peak may also differ from the normal situation. When discussing the influence of summer climate on the Enchytraeid population these facts may be of minor importance because they will not change the basic phenomena but only shift their occurrence to slightly different times, and it is possible that the normal curve may prove more symmetrical round the minimum than the one shown in Fig. 3. Another one-year cycle is being studied and until the results are available the question cannot be further discussed.

3. THE VERTICAL DISTRIBUTION OF ENCHYTRAEIDAE

In most habitats the vertical distribution of Enchytraeids is similar to that of the majority of soil animals, i. e. the density is greatest at the surface and decreases with depth. In particular this applies to all natural habitats with a dense plant cover and also to woodland habitats with a litter layer with or wihtout a plant cover.

The depth to which Enchytraeids penetrate varies in different stations depending on local circumstances. Single individuals have been found as far down as 70-75 cm below the surface on Sletten, a semi-natural pasture, where they are virtually living in the ground water zone. During the drought period in May-June 1954 they tended to migrate away from the very surface to deeper layers in order to escape the desiccation, however, the numbers obtained in the vertical sample series during this period were so small that the statistical significance of this migration could not be established except for the upper two five cm cores. Ordinarily the vertical distribution in arable land and in very dry places (e. g. st. 26) exceeds that in natural habitas with a plant cover. However, from the metabolic point of view the Enchytraeids of the deep layers can in most cases safely be neglected as they contribute a very small fraction only of the total population.

In this investigation it has been the object to study the total population in the different stations. Therefore, it was necessary to extend the sampling to such a depth that a reasonable fraction (~ at least 75 per cent.) of the fauna was obtained and to estimate the remaining fraction on the basis of special samples which were extended to such a depth that the type of vertical distribution throughout all inhabited horizons was known in the various stations at short intervals (~ 14 days to three weeks). As this part of the investigation was not designed as a study of the vertical distribution *per se* but only as a necessary supplement to the general sampling data this bulky material will only be briefly summarized here.

In Table 2 some selected typical data are presented.

TABLE 2

Nos. of Enchytraeids per core (mean of 2-15 cores from each depth). In italics the corresponding percentage of the population of the entire profile.

St.	Date	Depth, cm									
		0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	50-45	45-50
1	23. X	103	5	6	3	2	0	0	0	0	0
	1953	*86*	*5*	*5*	*2*	*2*	*0*	*0*	*0*	*0*	*0*
	25. III	146	27	30	28	6	—	0	1	0	0
	1954	*62*	*11*	*13*	*12*	*2*	—	*0*	—	*0*	*0*
	10. V	64	13	26	22	3	2	—	0	0	—
	1954	*48*	*10*	*20*	*17*	*3*	*2*	—	*0*	*0*	—
	19. V	43	2	1	—	0	0	—	0	—	0
	1954	*94*	*5*	*1*	—	*0*	*0*	—	*0*	—	*0*
	31. V	0.3	1.3	1	0.6	3	0.6	1.3	0.6	0.6	0.6
	1954	*3*	*13*	*10*	*6*	*29*	*6*	*13*	*6*	*6*	*6*
3	23. X	154	2	0.5	0	0	0	0	0	0	0
	1953	*98*	*1*	—	*0*	*0*	*0*	*0*	*0*	*0*	*0*
	31. III	90	10	5	8	5	0.3	0	0	0	0
	1954	*76*	*9*	*4*	*6*	*5*	—	*0*	*0*	*0*	*0*
4	28. X	685	3	1.5	0	0.5	0	0	0	0.5	0
	1953	*99*	—	—	*0*	—	*0*	*0*	*0*	—	*0*
35	3. IV	174	10	6	0.2	0.2	0	0	0	0	0
	1954	*92*	*5*	*3*	—	—	*0*	*0*	*0*	*0*	*0*
29	6. IV	286	43	9	2	2	0.2	0	0.4	0	0
	1954	*84*	*12*	*3*	*1*	*1*	—	*0*	—	*0*	*0*
20	24. III	40	15	12	11	6	2	1	0	0	0
	1954	*46*	*17*	*14*	*13*	*7*	*3*	*1*	*0*	*0*	*0*
16	13. XI	59	15	8	12	11	6	0.3	3	0.6	0
	1953	*51*	*13*	*7*	*11*	*9*	*5*	—	*2*	*1*	*0*
16	10. V	16	0.3	3	1.3	0.3	1	0	0	0.3	0.3
	1954	*71*	*1*	*13*	*6*	*1*	*4*	*0*	*0*	*1*	*1*

It will be seen that about 70-99 % of the total population are found in the upper five cm of the profile in most stations. In arable land (st. 19) the vertical distribution tends to be different, a smaller percentage occurring in the top five cm, while the density decreases more slowly with depth. The same applies to the very dry, almost bare sandy areas (e. g. st. 26) during the summer, while autumn, winter, and spring conditions more resemble the situation normally met with.

In order to study the micro-stratification of the fauna in the important upper horizons a few special samples have been taken. Table 3 shows the micro-stratification on Sletten (the Flat) on 6 Aug. 1954.

TABLE 3

Micro-stratification of Enchytraeids within upper 15 cm, Sletten, 6. VIII 1954.

Depth cm	Nos. per core (5 replicates)					Total	% distribution within 0-5 cm depth	% distribution within 0-15 cm depth
0-$1\frac{2}{3}$	109	67	41	236	107	560	81	61
$1\frac{2}{3}$-$3\frac{1}{3}$	28	6	13	22	23	92	13	10
$3\frac{1}{3}$-5	11	0	4	9	11	35	5	4
0-5	148	73	58	267	141	687		75
5-10	56	20	23	79	24	202		22
10-15	12	0	10	4	2	28		3

Thus, in habitats with a closed plant cover the density is seen to reach its maximum at the very surface and to decrease with depth. The rate of decrease varies between stations and in some cases (extremely dry, sandy areas) the maximum often occurs a little below the surface.

In general the vertical distribution of Enchytraeidae closely resembles that of freeliving nematodes (Nielsen 1949).

4. GENERAL DISTRIBUTION AND ABUNDANCE OF ENCHYTRAEIDAE

It will be obvious from what has been said in the previous chapters that the comparison of population densities is complicated by the fact that numbers fluctuate violently during the year. For fully reliable comparison to be made peak values should always be compared with peak values and minima with minima. In order to satisfy these requirements all-year values should be available from the habitats to be compared (because it must be assumed that, say, the position of peaks need not necessarily coincide in time in two fairly contrasting habitats). Therefore, the comparison of simultaneous values from two different habitats (with essentially unknown annual cycles) may in some cases lead to errors.

Although the author is fully aware of this complication a brief survey of a rather scattered sampling will be given. As the moisture status of the soil is known to be an important factor it has primarily been used as a basis of habitat classification.

As an introduction a brief description of the various stations is given. The discriptions are merely intended to give a general impression of the habitats studied. Only the conspicuous features are given, many details have been omitted because their importance for Enchytraeid density were not analyzed. The analysis of only a few factors would require a very painstaking and comprehensive investigation. On the other hand such stations have been studied which to the author seemed to be typical of the respective Danish habitats. In several cases further descriptions are given by Thamdrup (1947-48).

1. Description of remaining stations

I. Humid habitats

St. 7. A small spring near the Mols Laboratory. Grid reference (Thamdrup 1947-48) H 3. Samples taken among grasses and *Sphagnum* immediately at the spring.

St. 8. Same place but samples taken among *Vaccinium Myrtillus* and *Polytrichum commune.* In either station the soil is sandy with a fair amount of organic matter. Soil acid.

St. 9. Very dense grass at a spring near the Mols Laboratory; grid reference G 6. Eearly July 1954 the grass was cut for fodder.

St. 10. At the margin of a pond immediately at the Laboratory; grid reference H 6. Rich mull with luxurious growth of *Aegopodium, Urtica, Lamium, Chelidonium,* etc. under ash and willow. To some extent the area has been used as a dumping ground by two farms. The earthworm fauna is very rich, several species occurring, a. o. *Lumbricus terrestris.*

St. 11. At the border of a bog, Salissig, grown with *Carex,* spp. etc. Grid reference H 3.

St. 12. Peat bog with *Calluna, Erica Tetralix, Eriophorum* etc. Near Pindstrup, Jylland.

St. 15. Meadow at Engskrænten, Mols Laboratory, grid reference E 2. Raised Littorina sea bed. Hay-cutting takes place every year, no grazing. Fertilized 1954. Soil rich in organic matter. Vegetation tall but fairly open grass. Quite comparable with the Trough in geological and topographical respects.

St. 4 and *5.* See p. 13.

II. Pastures

St. 16. On the Flat of Sletten. Dense vegetation of *Sieglingia, Agrostis tenuis* and *Hylocomium squarrosum.* Elevation c. 280 cm. The station closely corresponds to st. 1.

St. 17. Sletten. This station is identical with Weis-Fogh's station "Pl. I". Reference is made to his description.

St. 18. Do. Identical with Weis-Fogh's st. "Pl. VII".

III. Leys

St. 19. Mols Laboratory. Raised Littorina sea bed. Grid reference C 5.

St. 20. Mols Laboratory. Moraine, sand with some clay. Grid reference I 7.

St. 21. State Experiment Station Blangstedgaard, near Odense, Fyn. Heavy clay soil in orchard with artificially maintained grass cover.

St.22. State Experiment Station Studsgaard, near Herning, Jylland. Grass field, heavily manured, in fertilizer experiment.

IV. Heathland

St. 23. Revlinghøj, Mols Laboratory. Grid reference F 5. Dense *Calluna* with a little *Empetrum*. Soil sandy with some fine material and organic matter.

St. 24. Near S. Engvej, Mols Laboratory. Grid reference F 4. Very similar to st. 23 but *Empetrum* is absent. Almost pure sand with very little organic matter.

St. 24a. Calluna heathland into which *Sarothamnus* has spread so as to become the sole dominant. Mols Laboratory. Grid reference E 5. Almost pure sand with very little organic matter.

St. 25. Stenhøj, Mols Laboratory. Grid reference I 5. Sand, almost without organic matter. Very open vegetation consisting of *Cladonia* spp., *Rhacomitrium, Polytrichum piliferum* with some *Hieracium pilosella, Jasione montana, Helichrysum arenarium.*

St. 25a. Same location but samples taken in dense *Calluna* tufts which have established themselves among the above mentioned vegetation.

St. 26. Corynephoretum, Mols Laboratory. Grid reference I 3. Almost pure sand with very little organic matter. Vegetation consisting of *Corynephorus canescens, Carex arenaria, Helichrysum arenarium, Jasione montana* and scattered tufts of *Calluna.* Samples from without the *Calluna* tufts.

St. 27. Rogeshøj, Mols Laboratory. Grid reference D 5. Raw humus with dense cover of *Calluna.* Description given by Weis-Fogh (1. c.) with two photos from the station (Figs. 28, 29).

St. 28. Same place but samples from under pure stands of *Juniperus* without field layer.

St. 29. Kithøj, Mols Laboratory. Grid reference E 5. Well developed raw humus near summit of hill. Vegetation: *Calluna* with mosses in between, especially *Dicranum scoparium* and *Hylocomium parietinum.*

St. 30. Same place but samples taken among *Vaccinium Myrtillus* which occurs in patches.

V. Woodland

St. 31. Alder swamp near the Mols Laboratory. Grid reference I 2. The ground is permanently wet and very rich in organic matter. The field layer is rich in species, *Chrysosplenium* being perhaps the most abundant one.

St. 32. Ash woodland. North end of Trough on Sletten. Grid reference E 3. See p. 12.

St. 33. Birch without field layer. Bordering on the bog Ålen. Grid reference B 3. Samples from birch litter with high root content.

St. 35. Oak woodland, Mols Laboratory. Grid reference E 4. Samples from oak litter.

St. 36. Beech woodland, Mols Laboratory. Grid reference F 1. Samples from beech litter without field layer.

St. 37. Beech woodland, Jernhatten, Jylland. Very rich calcareous mull with profuse field layer consisting of *Hedera helix*, *Anemone nemorosa*, *A. Hepatica*, *Mercurialis perennis*, *Ficaria verna*, *Asperula odorata*, *Gagea silvatica*, *Primula acaulis*, *Corydalis fabacea*, etc. Samples from beech litter. Earthworms very abundant.

St. 38. Spruce plantation, Provstbjerg near Mols Laboratory. Acid, sandy soil with needle layer and moss carpets.

St. 39. Same place. Pine plantation, open and with dense grass cover.

St. 40. Larch plantation. Acid, sandy soil with some organic matter. Mols Laboratory. Grid reference H 4.

St. 41. Oak woodland, Fjeldskov, Jylland. Raw humus with a field layer consisting of grasses.

St. 42. Spruce plantation, same place. Raw humus with thick needle layer and, in places, moss carpets.

St. 44. Beech woodland. Same place. Raw humus. No field layer.

St. 45. Spruce plantation, Høgildgaard near Herning, Jylland. Raw humus with dense moss carpets.

St. 46. Pine plantation, old, on raw humus. Field layer chiefly *Vaccinium Vitis Idaea.* Silkeborg Nørreskov, Jylland.

2. *Results*

The raw sampling data from the stations just mentioned have been brought together in Table 4. Each figure is the mean number of Enchytraeids per sample unit calculated from 1 sample consisting of 15 units. In a few cases more than one sample was taken, this has been indicated in the table. The exact sampling dates have not been given but the entire collection of data have been arranged in fortnoghtly intervals. Only the upper 5 cm have been included, and no corrections have been made for extraction efficiency or vertical distribution.

TABLE 4

St. no.	Mean no. of Enchytraeidae per sample unit (41.5 sq. cm area, 5 cm depth). Each figure based on 15 units																										Habitat
	Oct.		Nov.		Dec.		Jan.		Feb.		March		April		May		June		July		Aug.		Sep.		Oct.		
1	—	125	160	149	171	168	156	162				170	138	178[1]		65	33		26	134	166	114		253		145	main sts.
2		387		396		363		322				221			176		4	134		165		188		367		242	
3		371		338		309		281				195		137	8			10	41	66	77	51		66		71	
4			58		42	69	55	43					91	105	87[1]	89[1]	39	60	59	212	159	214		208		167	
5																117	120		163	406	380	372		461			
6													146	167	85		113	52	73	128	134	102		165		133	
7															155		113		145	74		59					humid
8																	97	133		207							
9																224		403	294	361	157	247					
10																	51				32						
11															299		52	119		271	395	339					
12				139										111					69								
15													123			8		48	52		128	122		102		129	
16															103				238	133		391					pastures
17			152															36		111	112	45					
18			154															391		342	354	337					
19																					26						leys
20															26				10	28		57					
21	81										65																
22	26			31																							
23			107											94				40		89	85						heathland
24			41											29				15		7	12						
24a			72											82													
25				8																							
25a				9																							
26		61		53								40															
27													191						88								
28													75		14				32	91[2]							
29		672											398	138		141											
30		467											118			107											
31																	98	47	37								woodland
32																	53		76	108	167	62				70	
33																121			94	173	140	114		217			
35													147														
36													44														
37														63		8		15	12					54			
38	318													131													
39	449													194													
40																		108									
41																32											
42	418						219	206						181		39			81		176	179					
44														145													
45																111											
46													121														

[1] mean of 30 units.

[2] mean of 45 units.

Utilizing the data of Table 4 and the vertical sample series one arrives at the following picture of the general distribution and abundance of Enchytraeidae.

I. Humid habitats

In humid habitats such as stations 4 and 5 (Fig. 2) the vertical distribution of Enchytraeids is practically identical throughout the year, high density prevailing in the upper 5 cm and decreasing with depth until disappearance about 30 cm down. No significant changes in the type of vertical zonation could be detected during the year. Some examples of the vertical distribution are given in Table 5.

TABLE 5

St.	Date	% of total population in depths				
		0-5	5-10	10-15	15-20	20-25 cm
4	28. X. 53	98	1.5	0.5	0	0
	31. III. 54	76	9	4	6	5
	9. VI. 54	77	11	8	4	0
	21. VII. 54	86	4	6	3	1
5	18. V. 54	88	11	1	0	0
31	26. X. 53	81	18	1	0	0
Mean of 16 series		81	13	4	0	2

The mean of 16 series from this category of habitats is given in the last row of the table. This percentage is used for the calculation of total population density. The reader who might want a more detailed picture of the seasonal fluctuation than the one given here will obtain the total population per sq.m on multiplying the numbers in Table 4 by $\frac{10^4 \times 10^2}{41 \times 81} = 301$.

In a bog with *Calluna* (st. 5) the population shows a peak value in late IX of 139 000 per sq.m preceded by a minimum (V-VI) of 36 000.

In the same place but under birch (st. 33) the density is lower on all sampling dates showing near-peak values of 65 400 (late IX) and 69 200 (early XI) with a minimum of 28 300 (early VII).

In the Trough (st. 4) the population between X. 53 and V. 54 fluctuated between 12 600 and 31 600 per sq.m with a tendency to increase. However, in V-VI the numbers decreased to 11 700 to rise again reaching a peak of 64 400 per sq.m in late IX.

Along the border of a spring little difference was found between the population density under grass and under *Vaccinium*, *Polytrichum* etc. The V-VIII densities vary between 17 700 and 62 000 per sq.m without clear tendencies.

Under grass covering a spring (st. 9) a minimum (late V) of 67 400 was found followed in late VI by a maximum of 121 000. A few days after this sampling the grass was cut and on sampling the station early VII the density had decreased to 88 500 (late VII 109 500; early VIII 47 200; and late VIII 73 700). Although no direct proof is at hand there is reason to believe that the sudden decrease was caused by the hay-cutting in some way or other, probably through exposing the soil surface to increased evaporation.

In the mull soil along the margin of a pond (st. 10) very low number were encountered; early VI 15 300 and early VIII 9 600 per sq.m.

A bog margin with dense grass turf (st. 11) showed a minimum of 15 600 in early VI preceded by a density of 90 000 one month earlier. The density increased to 119 000 in early VIII and 102 000 in late VIII. Thus there is indication that the autumn peak occurs earlier here than in the majority of stations.

The peat bog (st. 12) showed a near-peak value of 41 800 (late XI) and a near-minimum density of 20 800 (early VII).

In the alder swamp (st. 31) VI-VII densities of 29 500 to 11 100 were found.

Humid habitats are seen to harbour widely different densities, peak or near-peak densities range from some 40 000 to 140 000 per sq.m and minimum or near-minimum values from 12 000 to 90 000. The occurrence of a summer minimum is distinct (in spite of the fact that free water is never absent). Therefore, the minimum cannot solely be caused by desiccation. On the other hand the more clement environment is reflected in the fact that the percentage mortality during the period from autumn peak to summer minimum is definitely lower than in medium and very dry habitats. In the humid stations examined here it appears to vary between c. 15 and 80 %. Until pF or suction force measurements are available the exact relationship between mortality and availability of water cannot be discussed.

II. Pastures

In stations where an excess of free water is not normally present the percentage vertical distribution is influenced by drought periods. The influence is greatest in the surface layers and decreases with depth according to the degree of desiccation and the nature of the station. At least during some stage of desiccation practically all Enchytraeids in the upper 5 cm have been killed or forced to move further down while the original number is maintained farther down or sligthly increased due to immigration from above until the effect of the drought eventually reaches these deeper layers also. This feature is illustrated in Tables 2 and 6. It is quite distinct that the original population of deeper layers may increase somewhat through vertical migration. However, the phenomenon could not be studied in detail but from the metabolic point of view the complication is of little importance because of the heavy reduction of numbers in the (originally) densely populated surface layers. It will be seen from the Tables that although the migration is quite distinct the total number present in the entire profile is very small indeed compared with the pre-minimum values. Therefore the error committed by assuming the mortality to be confined to the upper 5 or 10 cm (depending on the time and station) and neglecting the downward migration is negligible from the metabolic point of view but, of course, not from the point of view of population dynamics.

TABLE 6

St.	Date	% of total population in depths				
		0-5	5-10	10-15	15-20	20-25 cm
1	3. VIII. 54	79	12	6	3	0
3	7. V. 54	13	59	25	1	2
	27. VIII. 54	69	23	6	1	1

In periodically dry pastures such as on the Ridge and the upper part of the Flat a pronounced seasonal variation occurs. The population density of the entire profile could, with a satisfactory degree of accuracy, be calculated outside the period when the population was at its minimum by multiplying the figures given in Table 4 by the same factor, 301, as employed in case of the humid habitats (actually the average percentage of the population in the upper 5 cm was calculated (from 19 series) to be 80, not 81 as the factor of 301 would imply, however, as the percentage is not significantly different from the one used earlier the same factor will be used here also).

On the upper part of the Ridge (st. 3) among grass, moss, and lichens the autumn peak of 1953 was calculated to be 111 500 per sq.m (early X) decreasing to a minimum a little above 2 400 in V-VI. 54 rising again to reach a peak of 21 400 in late X. 54. (Figures obtained after the conclusion of this investigation show that the population density is declining after this date). Thus we have a very dense population during the autumn of 1953 declining to a very small size during the summer of 1954 and never reaching the peak density present in the previous year. It is explained by the assumption that the population was damaged (through killing the adults and/or cocoons) to such an extent that the reproductive capacity was seriously impaired with. Future investigations are necessary in order to determine the time needed to reestablish an autumn population of the size occurring in 1953.

Where the vegetation consists of *Calluna* the autumn population of 1953 amounted to c. 117 000 (X-XI) decreasing to a little more than 1 200 in VII. 1954. However, in this station the population recovers and reaches a peak of 110 500 in late IX. 54. The fact that the summer reduction seems to be still more serious under *Calluna* while at the same time the following autumn peak appears to be unaffected makes it tempting to assume that the desiccation, after all, was less detrimental under *Calluna* because the cocoons present in the soil were not killed to nearly the same extent as under grass-moss. This problem is being studied and will be dealt with in a forthcoming paper.

On the Flat of the Plain st. 1 showed a 1953 autumn peak of 51 500 (early XII) decreasing to a summer minimum of 7 800 in early VII (i. e. somewhat later than in the very dry places, presumably because the desiccation was less severe). The succeeding autumn peak (late IX) was at 76 200, i. e. seemingly higher than the autumn peak of the previous year.

In another station on the Flat (st. 16) a near minimum value of 31 000 (early V) and a near maximum value of 117 500 (late VIII) was found.

In st. 17 on the Flat (= Weis-Fogh's st. "Pl. I") a near-peak density of 45 600 per sq.m occurred in early XI. 53 and a near-minimum density of 10 800 (late VI).

In st. 18 (= W.-F.'s st. "Pl. VII") on the lower part of the Flat the near-peak value (early XI. 53) was 46 300 (i. e. the same density as in the adjoining st. 17) however, no summer depression was detected, late VI the density was 117 500, late VII 103 000, early VIII 106 500, late VIII 107 200, and it can be added that a recent sampling (early XI) showed that the population had decreased to 82 000, i. e. higher than the previous year at the same time.

In the meadow st. 15 harboured an early IV density of 37 000 followed by a late V minimum of 2 400 increasing to a late X peak of 38 800.

Also in this category of habitats the figures are widely different in different stations. No general density figures for such habitats can be quoted. The peak or near-peak density varies between c. 21 400 and 117 500 and the minimum or near-minimum values are 1000-45 000. In the dry pastures the summer minimum is much below the peak value while in moister places the reduction is smaller, in one case (st. 18) the density even increased during the summer. In the dry places the summer minimum tends to occur earlier than in the less extreme stations.

III. Arable land

Several stations were in arable land. However, the material from these samples will be dealt with in a forthcoming publication, suffice it here to mention, that the highest densities were without exceptions encountered in grass fields, while fields grown with other crops were always poorer as regards the Enchytraeid population. As an example of the population density in such habitats the data from four stations will be briefly mentioned.

One feature of the Enchytraeid population in arable land is that the vertical distribution is distinctly different from the one in natural habitats. Relatively high densities occur to a greater depth than where the soil is not interfered with mechanically.

TABLE 7

St.	Date	% of total population at depths						
		0-5	5-10	10-15	15-20	20-25	25-30	30-35 cm
19	13. XI. 53	48	14	11	12	10	4	1
	10. V. 54	62	12	14	9	2	1	0
22	28. IX. 53	51	16	12	8	10	3	0

From the percentages given it will be obvious that a reasonable fraction of the total population could only be obtained through sampling down to 10-15 cm depth, i. e. by removing three successive slices of 5 cm each. Assuming the population in the upper 15 cm to represent 80 % of the total population the following densities were arrived at.

St. 19 (raised Littorina beach). Peak density (early XI. 53) was 24 000 per sq.m and minimum density 7 800 (early VIII. 54).

In another grassfield on moraine soil (st. 20) the minimum density (early V) was 6 800 and the maximum density (late VIII) 17 200.

At Blangstedgaard, in clay soil the near-maximum density was about 5 700 per sq.m and at Studsgaard in sandy soil about 3 000 per sq.m.

It is obvious from the samples quoted here and from the unpublished data available, that the population density of Enchytraeids in arable land is low throughout, lower than in practically all natural habitats studied. Furthermore there is good evidence that the density in grassfields is higher than under other crops.

IV. Heathland

In the section comprising the pastures one locality has already been discussed where *Calluna* is the sole dominant. This station could with good reason be considered an example of heathland, however, because of the historical situation and the obvious relation to the adjoining areas this station is considered a special type of pasture.

Several samples come from the natural heathland of the grounds of the Laboratory. In places where the organic matter is low, the soil almost pure sand and *Calluna* the dominant plant (st. 24) a peak density of 12 300 were found (early XI. 53) and a minimum density of 2 100 (late VII. 54).

When the organic matter content increases without changing the soil into a raw humus (st. 23) the density increases: Peak density 32 100 (early XI. 53), minimum density 12 100.

A recent invader, *Sarothamnus*, has in some places on pure sand replaced the *Calluna* completely and following its establishment higher population densities were found (st. 24a); in early XI 21 700 (in *Calluna* 12 300) and in late VI 24 700 (in *Calluna* 8 700).

In other places (st. 29) the organic matter content is increased and the soil forms a typical raw humus. This is noticeable in the fact that mosses, *Vaccinium*, *Polypodium* etc. become dominant plants together with *Calluna*. In such places striking differences in the Enchytraeid population are noticed. Among moss and *Calluna* the peak density was calculated at 202 000 (late X. 53) and the minimum density at 41 500 (late V. 54), while under *Vaccinium* the corresponding densities were 141 000 and 32 200 per sq.m.

In st. 27 with a less heavy raw humus the density was found to be lower: 57 500 in early IV and 26 500 in early VII. Where *Calluna* has been replaced by pure stands of juniper (st. 28) the corresponding densities were 22 600 and 9 600 with an absolute minimum of 4 200 in early V.

In very dry and sandy areas *Calluna* often succumbs for some reason or other. The space is aftewards occupied by an open vegetation with *Corynephorus* as the dominant with *Cladonia*, *Polytrichum* etc. It is mentioned here that the vegetation in such places is almost identical with that in st. 3. Sampling in such areas showed the Enchytraeid population density to be very low (sts. 25, 25a, and 26). The autumn peak was round 2 400 per sq.m while a late III density of 20 200 was calculated decreasing to some 800 during the summer. It is seen that the peak occurs during the spring and in addition to this aberrant situation the vertical distribution is also very different from the general picture. During the period autumn-winter the highest density occurs in the top layer while during the spring a downward shifting of the animals commences. In late III 47 % of the total population occurred in the upper 5 cm, 18 in the layer 5-10 cm, 14 in 10-15, 13 in 15-20 and 8 in 20-25 cm depth. In early VII 91 % occurred in the depth 15-20 cm, 7 in 20-25 and 3 in 25-30.

In the scattered *Calluna* tufts in such areas densities of the same order were found.

The type of vertical distribution in heathland with a dense plant cover is identical with the one hitherto found. The population densities in various types of heathland are different but there is a very clear connection between the amount of organic matter and the density of Enchytraeids. *When the organic matter content increases the Enchytraeid density behaves in the same way to reach its highest values in typical raw humus.* On the other hand a comparison between sts. 3 and 25 with practically identical vegetation but widely different geological history and water regime shows that vegetation *per se* is no reliable guide as far as Enchytraeid density is concerned.

V. Woodland

From very humid situations the data from an alder swamp have already been mentioned (st. 31). The VI-VII densities were 29 500 and 11 100.

In an ash woodland (st. 32) a minimum density of 16 000 (early VI) and a maximum density of 35 200 were found.

Densities under birch (st. 33) were lower than under *Calluna* in the same place: minimum 28 300 and maximum 65 400.

In oak woodland with litter layer (sts. 6 and 35) maximum densities of 44 000 and 49 500 were found and a minimum density of 15 600.

In a beech wood on sandy soil (st. 36) an early IV density of 13 200 was found, on calcareous clay (st. 37) the late IV density was 19 000, the late V minimum 2400 and the following late IX maximum 16 300.

In a beech wood on raw humus of rather poor quality (st. 41) the near-minimum density was about 21 400.

In a young spruce plantation on sandy soil (st. 38) the autumn peak density was 95 600 and in late IV 39 400, while a pine plantation on the same soil (st. 39) had the corresponding densities of 135 000 and 68 300.

A young larch plantation (st. 40) had a near minimum density of 32 300.

In an old spruce plantation (st. 42) the autumn peak density was 126 000 per sq.m decreasing to a summer minimum of 24 200.

The data from woodland show, that also this category is heterogeneous. Definitely low values occur in the good mull localities and surprisingly high densities in conifer plantations. Also from conifer plantations on raw humus righ densities have been reported but, unfortunately, only a small number of such habitats were studied. The relatively high densities in raw humus is in good agreement with the findings in heathland, and the relatively low values in mull soil corresponds well with previously mentioned data from st. 10 and from the arable land.

5. THE RELATION BETWEEN PLANTS AND ENCHYTRAEIDAE

It appears from the description that the vegetation of Sletten is in a state of flux. Juniper has established itself in many places and *Calluna* is sweeping over the area especially gaining a foothold round the already established junipers.

Thus, the transition from heavily to lightly grazed pasture conditions has been accompanied by a prompt change in the vegetation during which the original (pasture) grassland is first invaded by single junipers and patches of *Calluna*. At a later stage the *Calluna* tufts join and solid heathland results (which stage has already been reached on the eastern part of the Flat and on the southern part of the Ridge).

This clear-cut situation allows one to study very restricted areas (10-25 sq.m) where the elevation and all basic soil factors are identical while the original plant cover has been replaced by one or both of the recently established invaders.

This situation and its consequences for Enchytraeid density was analyzed in 4 stations on Sletten and in one outside this area.

St. 1. 24. X. 1953. 1 sample (of 15 units) from the *Sieglingia-Agrostis tenuis-Hieracium pilosella-Hylocomium squarrosum* turf and 1 from the *Calluna* tufts established 3 m from the station.

St. 2 and *3.* 12 samples covering a whole year (see Fig. 2).

St. 47. 5. XI. 1953. On the northern part of the Ridge. Elevation c. 380 cm. 1 sample from under three large junipers, 1 from the *Agrostis canina-Hieracium pilosella-Cladonia-Polytrichum piliferum* association forming the original turf, and 1 from patches of *Calluna*. All three samples were taken within an 8×4 m area.

St. 48. 3. XI. 1953. Eastern part of the Flat. Elevation 250 cm. Original *Carex demissa* turf almost completely replaced by dense *Calluna* with scattered junipers. One sample from under junipers and 1 from *Calluna*. Both of them taken within a 4×6 m area.

St. 27 and 28. Rogeshøj, Mols Laboratory. Grid reference D 5. One sample 14. IV. 54 and one 14. VII. 54. The situation may be somewhat different in this place compared with Sletten as the vegetational history is not exactly known. However, it is certain that the area was never cultivated. It is probable that once

Calluna dominated the entire area covered by the two stations, and that juniper is in the process of replacing the *Calluna*.

The results of the sampling are set out in the table below as mean numbers per core. Figures significantly different at the 5 % level are in italics. Comparisons can, of course, only be made in the horizontal direction within the single station. The corresponding densities per sq.m are obtained through multiplication by the factor 301.

TABLE 8

St.	Date	Grass	*Calluna*	*Juniperus*
1	24. X. 53	*125*	*211*	
2 & 3	29. X. 53	371	387	
	21. XI. 53	338	396	
	17. XII. 53	309	363	
	18. I. 54	281	322	
	28. III. 54	195		
	31. III. 54		221	
	21. IV. 54	137		
	6. V. 54	8		
	3. V. 54		176	
	9. VI. 54		4	
	17. VI. 54	10		
	25. VI. 54		134	
	1. VII. 54	41		
	19. VII. 54	66		
	23. VII. 54		165	
	2. VIII. 54	77		
	16. VIII. 54	51		
	17. VIII. 54		188	
	20. IX. 54	*66*	*367*	
	26. X. 54	*71*	*242*	
48	3. XI. 53		*173*	*97*
47	5. XI. 54	*181*	*279*	*68*
27 & 28	14. IV. 54		*191*	*75*
	14. VII. 54		*88*	*32*

Much more data would be needed in order to discuss the problem in detail. However, there is strong evidence that the invasion of *Calluna* is followed by a denser Enchytraeid population as compared with that of the original turf in dry and medium dry stations on Sletten. On the other hand following the establishment of juniper the numbers seem to decrease considerably, in st. 47 even far below that of the original grass turf.

The reasons for these changes were not studied but it can with a high degree of certainty be stated that no direct relationship between the invading plants and the Enchytraeids is operating. It is suggested that the moisture regime of the areas are changed such as to create a different environmental situation. The evidence for this is (1) that the summer minimum in st. 2 occurs about a fortnight later than in st. 3, (2) the population under *Calluna* was not damaged to nearly the same extent as the one in the original turf, which has not yet (XI. 1954) exceeded half the population density present in the autumn of 1953, and (3) the soil beneath juniper was in all cases much drier than that under *Calluna* presumably because of the heavier drain on the water resources exerted by juniper and because a larger percentage of the precipitation is being intercepted by juniper than by *Calluna*, thus never reaching the ground. This factor is well known in forestry practice although the author has not come across references to juniper in particular.

It is quite possible, even probable, that the invaders may cause other changes to take place through the changed nature of the litter layer, however, it is premature to discuss this as long as we have very little information on the food requirements of Enchytraeids.

6. LIMITS OF ERROR

The mean numbers of Enchytraeids per sample unit (0-5 cm depth) are presented in Table 4. To facilitate comparison with other investigations the mean number per sample unit was converted into the equivalent number per sq.m of the whole profile. Before doing so it was necessary to obtain some idea of the sources of error and their contribution to the total error of the density figures.

The systematic error inherent in the extraction technique was discussed in a previous paper (Nielsen 1952-53) and it is summarized here that its size cannot be stated under normal working conditions (a drawback that is associated with all techniques based upon the active emigration of animals from the cores). However, through special precautions efficiencies of practically 100 % can be attained under experimental conditions. The efficiency of routine extractions is probably somewhat lower, by which percentage is open to a guess, however, large scale extraction from confined spaces where also the patterning wsa studied (Nielsen 1954) gave evidence that the error must be small, and in all cases the populations are not overestimated which is important from the metabolic point of view. It is therefore assumed that the numbers extracted from the sample units agree well with or slightly underestimate the true number of live Enchytraeids present prior to extraction. *)

The vertical distribution of Enchytraeids in the soil profile was studied by special samples as mentioned p. 21 ff. This part of the

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*) After the completion of this paper Mr F. B. O'Connor (Bangor) informs me that the technique described by me (1952-53) in his hands gave results which were much lower than those obtained by him through a modification of the technique for extracting nematodes (Overgaard, 1947-48). The principle underlying this latter technique was found less satisfactory by me (1952-53). The reason why O'Connor finds lower numbers when using my method is quite obviously that too much heating has been applied or that the heating was too quick or the cooling was inefficient. He finds that "too many dead worms were found in the core, particularly in the litter layer". It will appear from my discussion of the sources of error inherent in the method (1952-53) that careful handsorting of 15 cores from which 513 worms had been extracted resulted in 6 additional worms, an error which can be neglected. Furthermore, the results published elsewhere (1954) could not possibly have been obtained if the efficiency was erratic. Theoretically a constant percentage loss might well be present, however, this would show up when handsorting is compared with extraction which is not the case. The technique described by me requires breaking in and adaptation until it gives satisfactory returns. In this laboratory this process took two years' of experimentation.

investigation is subject to the same systematic errors and to additional random errors. However, because of the fact that by far the greatest proportion of the total population was living in the upper 5 cm the influence of random errors is insignificant in this connection, the corrections introduced from the vertical sampling on the whole being small. Therefore the problem will not be discussed in detail. The analysis of vertical migrations would require a careful evalution of the random errors, however, this problem could not be solved satisfactorily because the investigation was so designed that only major migrations could, with some hope, be detected.

The random sampling error is a most important factor in the comparison of population densities in different stations and seasons. It has been mentioned (Nielsen 1952-53) that the S. D. is distinctly correlated with the mean no. per sample unit (x) and more recent data have fully confirmed this statement (Fig. 3). Using the entire body of data (except the vertical series and such horizontal series where, through accident or for other reasons) the sample did not consist of 15 units) an error graph was constructed. Before doing so the % S. D. was plotted against x (Fig. 4). Within the interval 0-210 Enchytraeids per unit the % S. D. was calculated for each of the intervals x = 0-9, 10-19, a. s. o. assuming a linear relationship between the two factors within such small intervals. At densities from 210-460 per unit the grouping had to be coarser because of the smaller number of samples having such high mean numbers. Table 9 summarizes the parameters for the intervals employed.

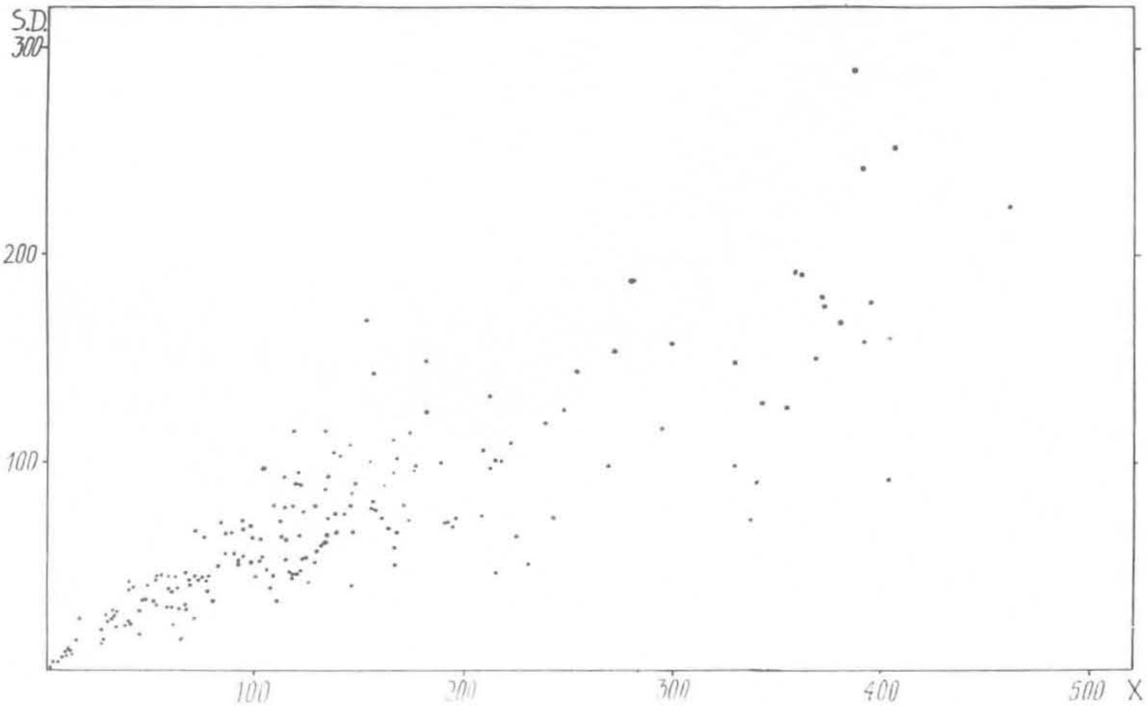

Fig. 3. Dot diagram of S. D. and mean number per sample unit (x)

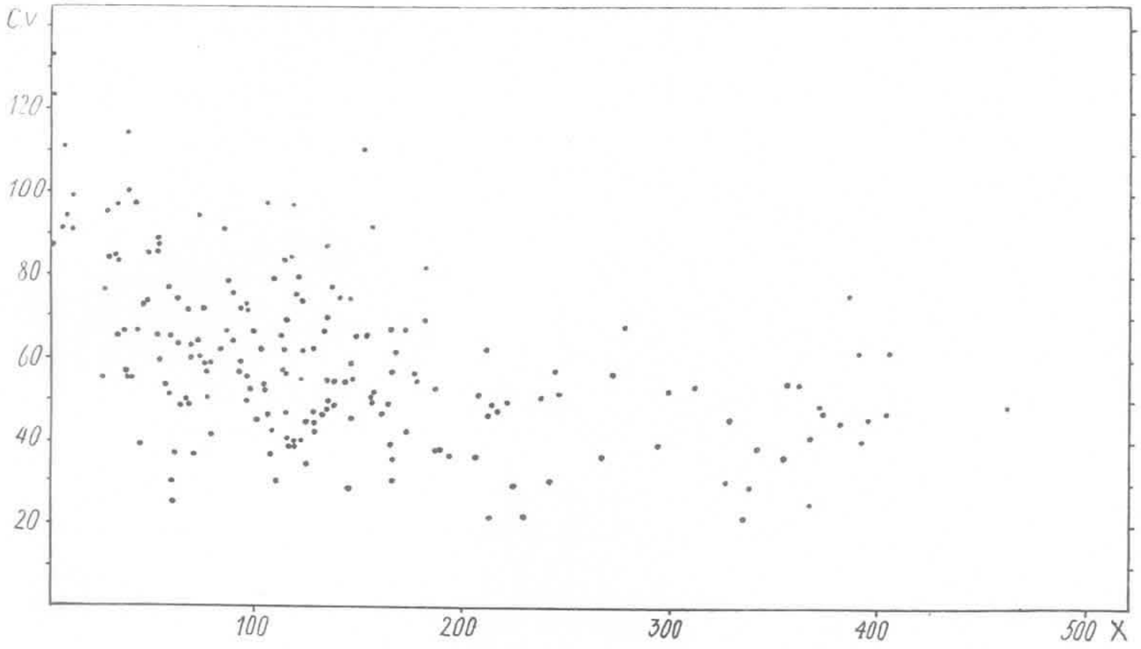

Fig. 4. Dot diagram of C. V. $(\frac{\text{S. D.} \times 100}{\text{x}})$ and mean number per sample unit (x)

As a side step it is mentioned here that the % S. E. per sample of 15 units decreases from 15 to 12 % only when the population density increases from 100 to 400 per sample unit. For routine work it might be suggested to use a smaller core size having, say, 100 Enchytraeids on an average as little is gained in accuracy for the extra cost of sorting and counting large numbers of Enchytraeids and accommodating larger cylinders on the water bath. However, it is difficult to avoid such half-wasted labour as the technique requires a high degree of standardization during the extraction process and as the population density in the individual stations undergo drastic fluctuations during the year.

The population densities quoted in this paper are assumed to be associated with the S. D. listed in Table 9 or read from Figs. 3 and 4, to which reference is made throughout.

TABLE 9

Population density		S. D.	% S. D.	S. E.	% S. E.
Nos./sq.m 1000	Mean no/unit				
1.22	5	5.6	113	1.5	29
3.66	15	14.7	98	3,8	25
6.10	25	21.2	85	5.5	22
7.92	35	27.8	79	7.2	21
10.98	45	33.3	74	8.6	19
13.41	55	38.5	70	10.0	18
15.85	65	43.5	67	11.2	17
18.30	75	48.7	65	12.6	17
20.72	85	53.5	63	13.9	16
23.19	95	58.0	61	15.0	16
25.60	105	62.0	59	16.0	15
28.05	115	66.5	58	17.2	15
30.50	125	70.0	57	18.1	14
32.90	135	75.5	56	19.5	14
35.40	145	79.5	55	20.5	14
37.80	155	83.5	54	21.6	14
40.20	165	87.4	53	22.6	14
42.60	175	91.0	52	23.5	13
45.10	185	96.0	52	24.8	13
47.50	195	99.5	51	25.7	13
50.00	205	104.5	51	27.0	13
52.40	215	107.5		27.8	13
-57.40	-235	-117.5	50	30.4	13
59.80	245	120.0		31.0	13
-64.60	-265	-130.0	49	33.6	13
67.10	275	132.0		34.2	12
-76.80	-315	-151.0	48	39.0	12
79.30	325	153.0		39.5	12
-93.90	-385	-181.0	47	46.8	12
96.30	395	182.0		47.0	12
-113.50	-465	214.0	46	55.3	12

7. THE SPECIES COMPOSITION IN DIFFERENT HABITATS

The study of this problem is complicated by the fact that the majority of individuals in a sample are immature and consequently cannot be identified with certainty, although in many cases they might be referred to genus.

This latter possibility was not utilized, as a rule, because no time was available for it. In the majority of samples the species composition of the mature individuals was analyzed and in this way a general idea of the occurrence of the various species was obtained. Only little will be said of the subject here because the data are not yet ripe for publication. During the investigation the taxonomy of Enchytraeids proved to be puzzling, especially as regards the genus *Henlea*. The whole problem has been studied by means of chromosome counts. Reference is made to the paper by Christensen and Nielsen (1955) where a preliminary account of the findings are given together with the species criteria used here.

It will be understood that the short review given below is of a preliminary nature.

1. The species composition in widely different habitats often exhibit a surprising similarity. *Fridericia bisetosa* (Lev.) is the dominant species in all stations on Sletten and in several other stations.

2. *Fridericia ratzeli* (Eisen) is widely distributed but while it occurs in all habitats ranging from water courses to dry sandy soil on the Ridge and raw humus it is rarely abundant, normally a few individuals are found in each sample. There are indications that it reaches its highest density in much the same places as the earthworm *Lumbricus terrestris*, i. e. in gardens and rich soils of the mull type near farmhouses, under pieces of wood lying on the ground etc.

3. *Mesenchytraeus beumeri* (Mich.) occurs in three station where it is regularly present but never reaching high densities: in the alder swamp of st. 31, in the soil, in the small streams and in old stumps; in st. 7 and 8 in and along the spring; and in the spruce plantation on raw humus (st. 42).

5. *Henlea* cf. *ventriculosa* (Udekem) is the dominant species in the grass field of st. 20 and under juniper in st. 28 (while it does not occur in the adjoining st. 27 under *Calluna*). In st. 28 it occurs together with *H.* cf. *nasuta* (Eisen). It also occurs in a small stream in the alder swamp of st. 31 and under bark of trees in various places, although the species concept may need revision.

6. *Bryodrilus ehlersi* Ude occurs in largest numbers under tree bark and in the wet soil and streams of the alder swamp of st. 31 but has also been found in several other stations on the Plain and elsewhere.

7. *Enchytraeoides sphagnetorum* (Vejd.) occurs in the same alder swamp, in the soil, in water, and under bark in wet decayed stumps. In addition it is present in the bog samples from st. 11.

8. *Fridericia leydigi* (Vejd.) occurs in the samples from Sletten, the springs and the alder swamp.

9. *Fridericia galba* was found in the samples from st. 27 and 28.

10. *Fridericia* cf. *hegemon* occurs in the wet area of st. 31 alder swamp.

11. Species of *Pachydrilus* were confined to the beach, not studied here. In wrack beds they occur with *Enchytraeus albidus* Henle which was not found in the samples examined.

12. *Enchytraeus buchholzi* Vejd. occurred in a single sample from a chicken pen.

It will be apparent from the exceedingly widespread occurrence of the species that the species composition cannot well be used to characterize the habitats. This applies in particular to the abundant species. Some of the rarer species may show more distinct habitat preference.

Because of the pronounced dominance of *Fridericia bisetosa* the stations on Sletten are directly comparable as this species contributes by far the greater proportion in all stations from the driest to the very wet ones.

8. THE BIOMASS OF ENCHYTRAEIDAE

It will be understood from the description of the weighing technique that it is laborious and time-consuming to obtain live weights of Enchytraeids with empty guts. Therefore, the collection of weight data is not of the size necessary for a detailed discussion of the biomass in all the stations. However, if the discussion is confined to the order of magnitude of biomass in different habitats only minor corrections will have to be introduced when a more comprehensive material is available.

In Fig. 5 the points indicate the mean weight of Enchytraeids from various stations at various times. The vertical lines indicate twice the standard error of the measurement and the figures refer to the different stations. In three stations measurements are available from different times of the year. In such cases the points have been connected by straight lines which, however, serve the only purpose of connecting values from the same stations. They have nothing to do with the true curve depicting the change in mean weight during the year.

In st. 1 the following weights were obtained: 24. X. 53: 0.078 ± 0.012 mg per individual; 21. IV. 54: 0.096 ± 0.020 mg; 10. V. 54: 0.108 ± 0.023 mg; 3. VIII. 54: 0.018 ± 0.004; 29. XI. 54: 0.071 ± 0.009 mg.

When the mean weights are compared with the population curve in Fig. 2 it is fairly simple to understand the underlying processes affecting the mean weight. In late Oct. the autumn peak is probably reached about a month ago and soon such low temperatures prevail that there is reason to believe that hatching has

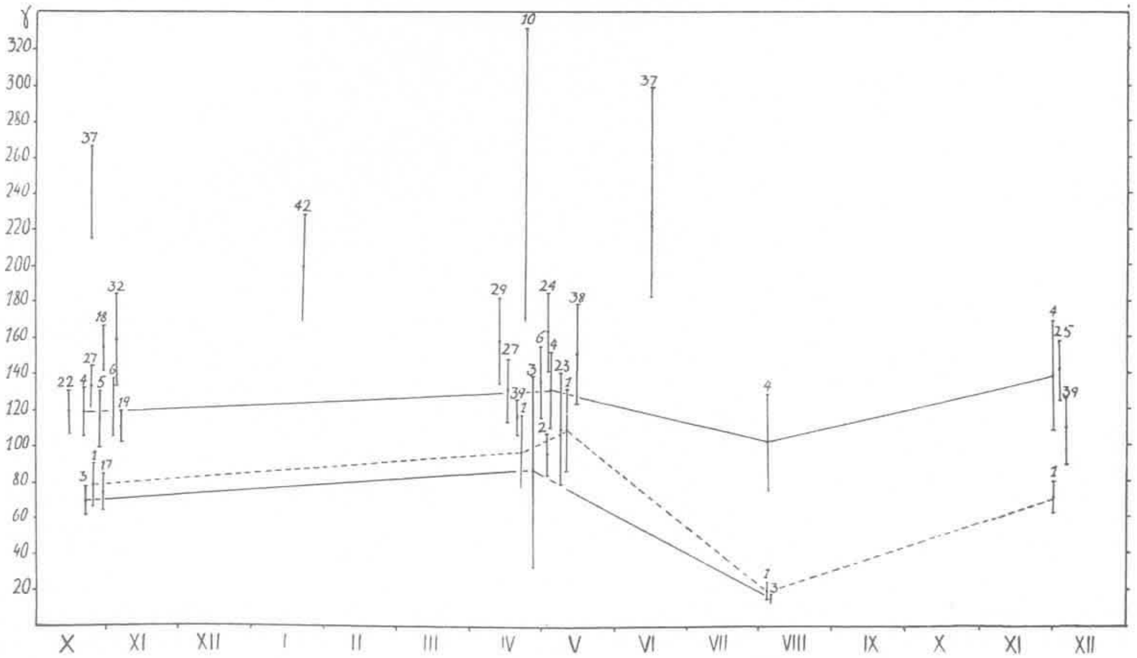

Fig. 5. Mean live weight of Enchytraeidae (in γ ± twice the S. E.) in various stations, numbers refer to description of stations in the text.

come to an end, i. e. there is no significant increase in numbers, rather the opposite, as some mortality must take place but apparently not a heavy one. The mean weight of 0.078 mg refer to a population the majority of which has hatched since about July 1953, but with a few survivers from the previous hatching period. During the relatively mild Nov., Dec., and Jan. some growth may have taken place but with temperatures round 0° C no excessive growth can be expected. During Feb. and first half of March the temperature was round ÷ 10° C and the ground entirely frozen with the consequence that all activity ceased. Towards the end of March the temperature rose above zero and sampling on 26. III. showed the population to be 51 200, i. e. a population of the same order of magnitude as in January. On 21. IV. the mean weight in the population was found to be 0.096 mg making it probable that some individual growth has taken place since last October. A fortnight later a still higher mean weight was found, 0.108 mg while the size of the population had decreased to 19 600, showing mortality to be heavy. During this period individual growth has taken place alongside with heavy mortality. Until early July the population declines rapidly to a minimum of 7 800 until a sudden rise commences towards mid-July leading up to an autumn peak of 76 000 per sq.m. During the first part of this phase the mean weight was found to be 0.018 mg or c. 17 % of the pre-minimum value. Newly hatched individuals weigh about 0.009 mg and an average weight of 0.018 would correspond to a population of newly hatched individuals with a very small number of full or half grown individuals which agrees well with what was actually found. The entire character of the population had changed radically after the minimum. During the period Aug.-Nov. the mean weight increased again to 0.071, i. e. to the same magnitude as in late Oct. of the previous year. During this latter period the mean weight probably changes in close accordance with the straight line in Fig. 5 connecting Aug.- and Oct. mean weights.

In spite of lacking details the weights obtained from st. 1 give valuable supplements to the curve depicting the fluctuation of population size, and they help very much to understand the underlying mechanisms. The most important feature is that the fluctuation in mean weight during the year fully confirms the fact that the great majority of Enchytraeids in st. 1 died during the summer minimum of 1954 without reaching maturity. By inference the same can be assumed to take place to a still larger extent in other habitats where the drought period was more severe as e. g. in st. 3 where the mean weight before and after the minimum was 0.084 ± 0.052 and 0.014 ± 0.003 mg. In st. 4 the decrease in mean weight after the minimum was smaller which is in good agreement with the fact that a smaller percentage of the mature and half-grown individuals were killed during the summer in this, less dry station.

Another interesting feature appears from Fig. 5, viz. that the populations in sts. 17 and 18 show widely different mean weights in Oct. 1953. The stations are only 12 m apart and in either case the population consists of *Fridericia bisetosa* almost exclusively. St. 18 is a good deal more humid than st. 17 (see description of stations on p. 12) and while the population density is identical in the two stations the growth conditions have been far better in st. 18. After the severe drought in 1954 the population size in st. 18 was about three times as high as in st. 17, indicating that also mortality is affected by the different environmental factors prevailing in the two stations.

In sts. 10 and 37 the mean weights seem to be entirely different from those of the remaining stations. The reason for this is probably of a different nature. The dominant species is in either case *Fridericia ratzeli,* which is much larger than the species dominating in the other stations, except *Mesenchytraeus beumeri* which, however, has never been found to be a dominant.

For sts. 1 and 4 it is possible to calculate reliable weights of the total population through the year. They are presented in the table below based upon the data of Figs. 2 and 5 and expressed in g/sq.m.

TABLE 10

Time	St. 1		St. 4	
	No./sq.m 1000	Biomass g/sq.m	No./sq.m 1000	Biomass g/sq.m
late X	37.6	2.9		
early IX	47.2	3.8	17.5	2.1
late IX	44.8	3.5		
early XII	51.5	4.0	12.6	1.5
late XII	50.5	3.9	20.8	2.5
early I	47.0	3.7	16.5	1.9
late I	48.6	3.8	13.0	1.5
late III	51.2	4.9		
early IV	41.5	4.0	27.4	3.2
late IV	53.5	5.8	31.6	4.1
early V			26.2	3.4
late V	19.6	2.1	26.8	3.5
early VI	9.9	1.1	11.7	1.5
late VI			18.1	2.4
early VII	7.8	0.8	17.8	2.3
late VII	40.2	0.8	63.7	0.6
early VIII	50.0	1.0	47.8	1.6
late VIII	34.3	0.9	64.5	7.0
late IX	76.0	3.5	62.5	7.4
late X	43.6	2.4	50.2	6.9

In the remaining habitats similar satisfactory determination of the seasonal variation in biomass could not be made. However, from the general seasonal events it will be understood that the mean weight during the autumn is ordinarily intermediary in size between the mean weight prior to and just after the summer minimum. Therefore, one might assume the autumn mean weight to be roughly valid through the year excepting the summer months (June-August incl.) and consider the autumn-winter-spring population alone disregarding the summer population which would be small in many habitats. It is admitted that errors of unknown size are introduced by such a procedure but for de purpose of obtaining some idea of the order of magnitude of Enchytraeid biomass during the greater part of the year they seem to the author to be a good substitute for no value at all.

In Table 11 such values have been calculated for a number of habitats, it being understood that the figures should not be considered preliminary.

TABLE 11

Habitat	Biomass g/sq.m		Station
	Peak	Pre-minimum	
pasture, dry	7.8 (1953)	2.4	3
	1.6 (1954)		3
pasture, dry	3.3 (1953)		17
pasture, medium	2.9 (1953)	5.8	1
	3.5 (1954)		1
pasture, humid	2.1 (1953)	3.5	4
	7.4 (1954)		4
pasture, humid	7.1 (1953)		18
ley	0.4 (1953)		22
Calluna heathland 1 % org. matter	0.3 (1953)		25
Calluna heathland c. 1 % org. matter	1.8 (1953)		24
Calluna heathland 2-3 % org. matter	3.2		23
Sarothamnus heathland	3.3		24a
Calluna heathland, raw humus	26.7		29
Calluna, bog	15.8		5
ash woodland, mull	5.0		32
oak woodland, mul	5.9		6
beech woodland, calcareous mull	3.8		37
ash, rich mull		3.7	10
pine plantation, young, sand.	14.8		39
spruce plantation, old, raw humus	25.0		42

No far reaching conclusions should be drawn on the basis of a material of this nature. Suffice it here to say that the biomass of Enchytraeids varies very much during the year and often between different years in the same station. While in most cases there is no obvious relationship between the nature of a habitat and the Enchytraeid biomass contained in it a few facts seem well established.

(1) In raw humus carrying an ordinary *Calluna* heathland or planted with conifers the population size and its biomass is higher than in most other habitats, and in heathland where there is no raw humus there seems to be a direct relationship between the amount of organic matter and biomass of Enchytraeids. In dry stations the numbers and biomass decrease while moisture favours a large biomass.

(2) In arable land the population density is low, and so is the biomass. Highest values were found in grass fields but even there, the biomass is far below that occurring in practically all other habitats.

(3) In woodland on mull soils the population density is apparently low, but the species and age group composition is such as to produce biomass figures somewhat higher than one would expect from the raw density figures.

9. COMPARISON WITH OTHER INVESTIGATIONS

Hitherto the Enchytraeids have not been studied very much in ordinary soils. Reynoldson (1939a, 1939b, 1943, 1947a, 1947b, 1948) studied the Enchytraeids of sewage bacteria beds and contributed valuable information on the population in such habitats.

The soil fauna proper has chiefly attracted the interest of workers dealing with taxonomical problems. Several pieces of information can be found in papers by Backlund (1946, 1947), Ude (1929), and others.

From a quantitative point of view two papers deserve to be mentioned namely those of Jegen (1920) and Moszynski (1930).

The chief findings of Jegen are reproduced in the following Table 12 giving the relationship between soil type (original classification), season and density of Enchytraeids per sq.m.

TABLE 12

Season	Tonboden	Lehmboden	Lehmiger Sandboden	Sandboden	Humusboden
1. Spring	vereinzelt	60-160	2750-6400	6900-9000	30000-70000
2. Summer					
a. dry	—	28-75	1400-2300	2600-4900	11800-16000
b. wet	—	70-300	3000-7000	6500-8500	28000-50000
3. Autumn	—	100-450	5000-10000	7000-11000	60000-150000
4. Winter	—	800-1600	2000-8000	6800-9400	50000-120000

Although Jegen's densities are lower throughout than those reported here there is a surprising agreement between the seasonal trends found by him and those described here.

The discrepancy between the absolute densities reported by Jegen and the present author are most conspicuous in the category of sandy soils from where the bulk of my data were collected. On the whole the densities reported here are about ten times as high as those given by Jegen while in the case of organic soils the highest peak value reported here is 202 000 per sq.m as compared with the value of 150 000 reported by Jegen. However, it must be remembered that only very few raw humus localities were examined by me. There is no doubt that even higher densities would be encountered if the chief activity had been centered on such soils, which will be done in a later publication.

The densities reported by Moszynski are more difficult to compare with those reported here. The best basis for comparison is probably afforded by his table 9 which is copied here (Table 13) (maintaining the original legends) but recalculating his densities to sq.m instead of sq.dm).

TABLE 13

No.	Milieu	Mean no. pr. sq.m	Variation in density	No. of species
1	Sable, couches superficielle	300	0-600	5
2	Sable, couches plus profonde	1000	0-2000	5
3	Sable, melé de débris végétaux	10000	1000-26000	10
4	Champs cultivés, sable avec humus	8000-14000	0-16500	6
5	Détritus végétal	15000-25000	7000-80000	9
6	Parcs et vergers	15000-20000	1000-31000	7
7	Prairies tourbeuses avec humus	20000-35000	5000-72000	14
8	Terres humides et marécages	3000-7000	0-18000	7

Again in this case the densities are much lower than those found by me, and in either case it is probable that the greater part of the explanation is to be found in the technique. However, the majority of Moszynki's sample were taken during the summer months at which time the density is at a minimum (in Switzerland and in Denmark). This factor may also be partly responsible for the lower densities reported.

On the question of vertical distribution Moszynski arrives at practically the same results as those outlined in this paper: (1) in natural grasslands (prairies) the majority of the fauna is concentrated in the very surface layer, (2) in arable land Enchytraeids tend to maintain a relatively high concentration also in somewhat deeper layers, and (3) in pure sand the maximum is below the surface layer, the density decreasing up- and downwards.

The habitats studied by Moszynski were selected in a somewhat different way than in the present investigation, therefore it is difficult to compare the findings directly, however, the result arrived at by Moszynski, that the greatest densities are met with in decaying plant matter (détritus vegetal) and organic soils (prairies tourbeuses avec humus) are not at all incompatible with my conclusions.

The distribution of different species in the various habitats is discussed in some detail by Moszynski. However, my material cannot be used for any direct comparison because of various shortcomings. It is quite distinct from Moszynski's table on p. 104-5 that the majority of species has a very wide range as regards habitats. There is good agreement between his and my conclusion that *Fridericia bisetosa* may be dominant in practically all habitats, on the other hand *Enchytraeus albidus* seems to be more widespread in the Polish material, and the same applies to *Enchytraeoides sphagnetorum*, which in my material was confined to wet places. *Mesenchytraeus beumeri* is not reported by Moszynski at all.

In table 11 Moszynski presents some data on the volume of Enchytraeids per sq.dm. They range from 3.1 mm^3 to 650 mm^3. If the volumes are converted roughly to weights by assuming the specific density to be unity 1000 individuals in station 1 of his table would weigh c. 3 mg, and in st. 20 60000 individuals would weigh 65 g, i. e. the mean weight would be c. 1.1 mg.

Mean weights as would be implied in the first mentioned station might well occur, but a mean weight of 1.1 mg as would be required in the last mentioned station could not possibly result from the analysis of a natural population with a great majority of young and immature individuals therefore the present author is forced to believe that these volumes are not representative of the true population mean. From the description of the technique by means of which they were obtained, it is evident that they cannot be more than tentative, and, indeed, Moszynski does not attach any great value to the data assembled.

10. COMPARISON WITH OTHER SOIL ORGANISMS

One aim of soil zoology must be to provide some idea of the relative proportions of the total biomass contributed by the different members of the fauna, to consider their contributions to soil metabolism and to circumscribe their »jobs«. However, this is a most intricate task and one should always exert a high degree of scepticism because of the many internal cycles within the one obvious cycle.

In spite of the difficulties it will be necessary to tackle the problem and hope for gradual improvements of the results arrived at by different workers.

In a previous paper the author undertook a census of freeliving nematodes in a number of habitats. The present study was designed such as to enable a direct comparison to be made with the results obtained in this group of soil animals. Indeed, a number of stations are identical in the two studies, and where not completely identical they are in many cases nearly so.

TABLE 14

Habitat	**Enchytraeids**		**Nematodes**		**Microarthropods**	
	Nos./sq.m 1000	Biomass/m^2 g	Nos./m^2 mill.	Biomass/m^2 g	Nos./m^2 1000	Biomass g
st. 4	10-64	0.6-7	1.5	3.1		
17	11-46	1-3	10	13.5	48	2
18	46-117	3-7	10	14	34	
25	1-20	0.1-2	0.2	1		
23, 24, 25a	2-30	0.2-3	0.8	2		
15	2-40	0.2-4	1.2	2-3		
Calluna raw humus	40-200	5-25	1-3	1-5		
29	50	7		2	300	4-5
conifer plantations	24-126	3-25	1-2	4-5		11

In the stations 17 and 18 on Sletten an increasing amount of data have been and are being collected. Weis-Fogh (l. c.) contributed data on mites and collembola, the present author data on nematodes and in this investigation the stations were again utilized for the Enchytraeid census.

In Table 14 it is attempted to put together some relevant data compiled from Weis-Fogh (1947-48) and Nielsen (1949) concerning number and biomass of nematodes, mites, collembola, and Enchytraeids from identical or comparable habitats. The figures are approximate and only orders of magnitude should be considered.

From this comparative material it will be seen that while the numbers present of the three animal groups are very different, nematodes to be counted by the million and Enchytraeids, mites and collembola by the thousand, the biomass is quite comparable. Normally they will each contribute a few grammes per sq.m in mineral soils varying very much according to the habitat.

In raw humus the picture is totally changed, here mites and collembola are much more important than nematodes, and Enchytraeids attain their greatest abundance and biomass.

In a previous paper it was shown that nematodes are most plentiful in mineral soil where the importance of mites and collembola is reduced. A conclusion of the present study is that *Enchytraeidae belong to the ecological group of soil animals most abundant in organic soils.*

In view of the fact that the other oligochaete representatives, Lumbricidae, are distributed in a way similar to nematodes, it is most interesting to find that in this respect Lumbricidae and Enchytraeidae are entirely different. This will be obvious from the fact that high Enchytraeid densities were found in acid heathland, especially on raw humus and in conifer plantations, habitats which are very poor in earthworms, and in this country only inhabited by *Dendrobaena octaedra.* Also Bornebusch (1930) arrives at the largest Enchytraeid biomass (1.6 and 1.2 g per sq.m) in raw humus (beech). Because of the fact that the technique employed by Bornebusch is inefficient when used for the extraction of Enchytraeidae the biomass per se is far too low but when compared with the earthworm biomass quoted from various of his stations it will be seen that in the raw humus localities the biomass of Enchytraeidae is of the same order as that of earthworms (which is probably correct) or even exceeding it, while in the mull localities the earthworms contribute a biomass 10-100 times larger than the biomass of Enchytraeidae.

On the other hand low numbers of Enchytraeidae were found in the calcareous clay beech wood of st. 37 where earthworms are extremely abundant. The same applies to st. 10 where *Lumbricus terrestris* is plentiful together with other species.

Even on a small area, like Sletten, the two groups are very distinctively distributed. The highest earthworm figures are obtained from st. 4 where the number of Enchytraeidae was relatively low, while in the higher parts, especially with *Calluna*, the earthworm density is low and the Enchytraeid population dense, at least during the part of the year when the moisture status is favourable.

Thus there is reason to consider the ecological status of Enchytraeidae very different from that of Lumbricidae. Although the Enchytraeidae occur plentifully in mineral (mull) soil they seem to attain much larger density and biomass in the raw humus where their importance is probably greater not only because of their larger numbers but also because few soil animals seem to prefer this soil type.

11. SUMMARY

The present paper results from a one-year study on the ecology of Enchytraeidae in about fifty stations representative of a wide variety of Danish habitats.

The material underlying the investigation and the methods employed during the analysis are described in chapter 1.

Chapter 2 deals with the seasonal variation throughout a year in 6 stations which were studied in greater detail. It appears that maximum density occurs during the autumn while a pronounced minimum prevails during the early summer. It is likely that the position in time of the minimum will be somewhat later (towards mid-summer) in "normal"years. The summer of 1954 was exceptional in several meteorological respects, especially as to rainfall and temperature.

The summer minimum imply a mortality from 30 to 90 % of the autumn population in the different stations, and the majority of individuals seem to die before reaching maturity. The factors causing this mortality could not be fully identified although part of the mortality could be attributed to desiccation.

The vertical distribution of Enchytraeidae within the part of the profile where they occurred at all agrees well with the one found in freeliving nematodes. In most habitats the greater concentration occurs in the very surface layer, decreasing further down until the population almost disappears about 30 cm down. In arable land the density decreases more slowly with depth and in very dry stations the maximum may be somewhat below the surface, especially during the summer.

The population density of Enchytraeidae varies very much within even closely similar stations. The peak or near-peak density in most stations was of the order of 50 000-100 000 per sq.m.

Few general conclusions concerning the relation between edaphic factors and the density of Enchytraeidae could be drawn.

(1) humid habitats seems to favour higher population densities (with a relatively small summer mortality),

(2) raw humus is apparently a much more favourable substratum than mull. The highest density (202 000 per sq.m) was encountered in *Calluna* heathland

on raw humus, but also conifer plantations on this soil type have a dense population of Enchytraeidae,

(3) arable land seems invariably to harbour a low population density.

The changes in the density of Enchytraeidae following on a recent plant succession (grass-*Calluna-Juniperus*) were studied. The spread of heather was accompanied by higher density while the establishment of juniper caused the numbers to drop considerably again.

The random errors of the density figures are small. When the density is about 30 000 per sq.m the S. E. per sample af 15 units is about 15 % while it drops to 12 % when the density increases to about 100 000 per sq.m.

The species composition in the habitats studied is not very different when the dominant species are considered. *Fridericia bisetosa* is by far the commonest species. Certain species seem to be confined to humid habitats while *Fridericia ratzeli* is more abundant in typical mull soils.

The biomass of Enchytraeidae ordinarily amounts to a few g per sq.m (autumn - spring), i. e. of the same order as the biomass of freeliving nematodes and mites + Collembola. In raw humus the biomass may be about 25 g pr. sq.m, and even higher weights can reasonably be expected because only few raw humus stations were studied.

Thus the Enchytraeidae belong to the ecological group of soil animals which is most abundant in raw humus. In this respect they are similar to mites and Collembola and very much different from their close allies, Lumbricidae (except *Dendrobaena octaedra*). Also freeliving nematodes are more abundant in mull soils.

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